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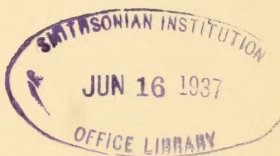
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# SMITHSONIAN

## MISCELLANEOUS COLLECTIONS

VOL. 95



"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES,  
AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—SMITHSON

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## ADVERTISEMENT

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C. G. ABBOT,

*Secretary of the Smithsonian Institution.*





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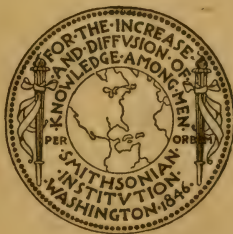
SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 1

## Roebling Fund

OBSERVING THE SUN AT 19,300 FEET ALTITUDE,  
MOUNT AUNCONQUILCHA, CHILE

BY  
C. P. BUTLER



(PUBLICATION 3379)

CITY OF WASHINGTON  
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### OBSERVING THE SUN AT 19,300 FEET ALTITUDE, MOUNT AUNCONQUILCHA, CHILE

By C. P. BUTLER.

If solar observations could be made on the moon, the readings of a silver-disk pyrheliometer alone would give us the solar constant. Since this is impossible, we may approximate the solar constant by making radiation measurements at different altitudes. The highest observations made heretofore with the silver-disk pyrheliometer were those taken by Dr. C. G. Abbot on Mount Whitney, 14,500 feet.

I was invited by the International High Altitude Expedition to join them at their highest station for the purpose of making solar observations. Their object was to measure the effects of extreme high altitudes on the human body mainly through the analysis of blood taken from the men at different altitudes. All the experiments were made in northern Chile, culminating on Mount Aunconquilcha.

Ollague is a small town on the frontier between Chile and Bolivia, situated on a great level altiplano stretching many miles from the sulfur peaks. The terrain is broken into rough hummocks of salt incrustations, with here and there small salt-water marshes. It was here that the expedition kept the four railway cars which housed their heavier instruments.

I stayed the first night in one of the sleeping cars in Ollague, and the next morning I left by motor truck for the Quilcha Camp where most of the men were stationed. The truck was filled with a heterogeneous load of bundles, trunks, beds and bedding, and tools, and its passengers included 12 miners and 2 women. On top of the load were precariously perched the pyrheliometers and the theodolite, with the assurance of one of the men that he would look after it. With the load nearly double the truck's capacity and the bad curves in the road, it seemed to me that every sway would pitch some boxes off. However, nothing happened to the instruments—just to my nerves.

The Quilcha Camp is located at an altitude of 17,400 feet and is said to be the highest permanent human settlement in the world. The word "permanent" must not be taken too seriously, however, because the men and women who live here suffer from diseases peculiar

to the altitude, and consequently the population continuously shifts. Only high wages induce the men to live here, and as a rule they stay only a few weeks, after which, with a little money, they leave for the lower altitudes. Many of the men take their families with them, but so far as is known no woman has given birth to a child at this altitude. Most of the children in the camp were born in Ollague (12,000 ft.).

The day after my arrival in camp, I set up the pyrheliometers and ran a long series of observations here. The sky was very clear, with only a few wisps of cirri visible. On my second day in camp I made arrangements to go on up to the mine. Mules were available, and with the help of one of the guides I got all the instruments roped on one of the mules. We rode all the way to the top, and even with the loads and our constant prodding the mules did not seem to suffer from the height. Horses become so nervous that they cannot be used here.

We arrived at the sulfur mine at about 10 o'clock in the morning, and there I found two boys to help me carry the instruments to the top of the mine. There were no boxes or tables available to hold the pyrheliometers, so I chose a ledge of ice covered with sulfur. Little blocks of yellow sulfur served nicely to level up the legs of the pyrheliometers. Below this was a sloping ledge of clear ice on which I stood. I set up the theodolite on the ice; the only trouble encountered was that the ice would melt under the legs, and the instrument had to be releveled each time a reading was taken. This was due partly to the weight and partly to the fact that the brass points on the legs were black and served as very good absorbers of the sun's rays. Fortunately the sky here also was very clear, and there was no wind during the observing.

All readings were made with a stop watch whose second hand had an eccentricity of less than  $\frac{1}{3}$  second as tested with a standard pendulum used in our regular observations. A sun reflector was attached to the back of the telescope for the solar altitudes. The constants of pyrheliometers No. 29 and No. 30 were determined before and after the trip. The silver disks were not touched during the journey. Before each set of observations the three screws holding the silver disks were loosened; after the observations they were again tightened. No severe jar or bump was given the pyrheliometers throughout the trip. On the return from the mine the theodolite box fell off the mule, but before it could roll down the mountain, the muleteer jumped from his mule and caught it. Fortunately no harm was done.

The results of the instrumental data were not apparent to the senses. At the mine even during the middle of the day the temperature hardly rose above freezing, even though Aunconquilcha is nearly 200 miles

north of the Tropic of Capricorn. We all wore heavy clothing, stocking caps, mittens, and heavy shoes. Despite the cold, one burned severely in a few hours without the protection of a sunshade. The natives are ordinarily a light brown color, but the men who work the mine were burned almost black. The data show that the amount of

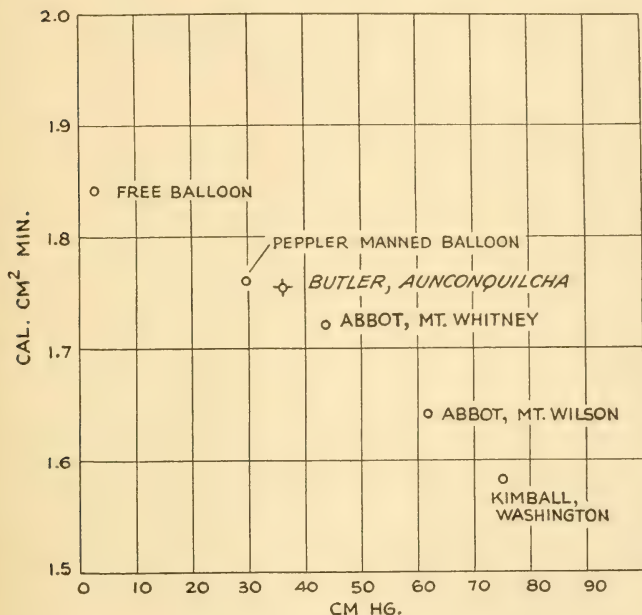


FIG. 1.—Pyrheliometry at high altitudes.

solar radiation here is greater than ever experienced at sea level, but the only way this could be felt was in a feverish feeling about the nose, cheeks, and neck.

At air-mass 1.40 the pyrheliometers gave a mean value of 1.663 calories per square centimeter per minute. A reduction of this to what it would be at vertical sun and at the earth's mean distance from the sun becomes 1.753 and shows that the value lies nearly in line with the plot in figure 58 in the *Annals of the Astrophysical Observatory*, volume 4.

*Summary of the Readings Taken on the Aunconquilcha Expedition.*

July 4, 1935		July 5, 1935	
Mine Camp, 17,400 feet.		Aunconquilcha, 19,300 feet	
m	Pyrh.	m	Pyrh.
1.79	4.338	1.46	4.555
1.79	4.367	1.46	4.555
1.77	4.371	1.45	4.509
1.76	4.464	1.45	4.565
1.74	4.355	1.43	4.528
1.74	4.401	1.43	4.557
1.72	4.395	1.43	4.606
1.71	4.389	1.42	4.611
1.57	4.485	1.41	4.533
1.56	4.431	1.41	4.582
1.55	4.476	1.41	4.599
1.55	4.468	1.41	4.644
1.54	4.415	1.40	4.596
1.53	4.428	1.40	4.608
1.52	4.443	1.39	4.532
1.52	4.425	1.39	4.543
1.42	4.453	1.39	4.586
1.41	4.511	1.39	4.620
		1.40	4.529
1.97	4.217	1.40	4.593
1.98	4.301	1.40	4.580
2.01	4.226	1.40	4.627
2.02	4.317		
2.05	4.283		
2.06	4.284	Pyrheliometer Constant (.3629)	
2.09	4.190		
2.10	4.245		

In order to obtain the value of the solar radiation at air-mass 1, a comparison of the slopes of the pyrheliometer at Montezuma, the Mine Camp, and at Aunconquilcha was made. Owing to the sun's declination, air-mass 1.39 was the lowest possible at this time of the year.



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VOLUME 95, NUMBER 2

LETHAL EFFECT OF SHORT WAVE LENGTHS  
OF THE ULTRAVIOLET ON THE ALGA  
*CHLORELLA VULGARIS*

(WITH TWO PLATES)

BY

FLORENCE E. MEIER

Division of Radiation and Organisms,  
Smithsonian Institution



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# LETHAL EFFECT OF SHORT WAVE LENGTHS OF THE ULTRAVIOLET ON THE ALGA *CHLORELLA VULGARIS*

By FLORENCE E. MEIER

*Division of Radiation and Organisms, Smithsonian Institution*

(WITH TWO PLATES)

## INTRODUCTION

Quantitative investigation of the lethal action of eight wave lengths below the short-wave limit of ultraviolet irradiation in nature on the unicellular green alga *Chlorella vulgaris* has been reported in two previous papers (Meier, 1932, 1934). A study was made in these papers of the response of the alga to 12 wave lengths of a mercury vapor arc ranging from 2536 Å to 3650 Å, which was made possible by the use of a fused quartz spectrograph. By means of a crystal quartz spectrograph, the research has now been extended to the lethal effect of 21 wave lengths in the ultraviolet ranging from 2250 Å to 3130 Å on the same alga.

The spectroscopic manipulations and physical measurements were made by Dr. E. D. McAlister, of the Division of Radiation and Organisms.

I am deeply grateful to Dr. C. G. Abbot, Secretary of the Smithsonian Institution, for his encouragement and assistance in the interpretation of the results of the experiments here reported.

## EXPERIMENTAL PROCEDURE

*Chlorella vulgaris* has proved to be well adapted to this type of research because of the spherical shape of its single green cell and the uniformity and speed with which the cells, multiplying by oval or elliptical spores, cover the surface of an agar plate. This unicellular green alga consists of a spherical cell containing a parietal chromatophore and one easily visible pyrenoid. The diameter of the cell is usually  $3\mu$  to  $5\mu$ , although some giant cells exceed  $10\mu$ . This alga has been maintained in pure culture in my collection for 5 years.

The nutritive solution in which the algae were grown is Detmer  $\frac{1}{3}$ , a modified Knop solution, made up in the following proportions and then diluted to one-third:

Calcium nitrate .....	1.	gram
Potassium chloride .....	0.25	"
Magnesium sulfate .....	0.25	"
Potassium acid phosphate.....	0.25	"
Ferric chloride .....	0.002	"
Distilled water .....	1.	liter

The surface of a glass plate of dimensions 8 x 10 cm was ground so as to retain the agar poured on it. This plate was placed in a large petri dish 15 cm in diameter and after sterilization in the autoclave at 15 pounds pressure for 20 minutes was covered with a layer about 4 mm thick of Detmer  $\frac{1}{3}$  agar 2 percent and then sterilized a second time.

When the agar had gelled, a heavy suspension of green cells of *Chlorella vulgaris* that had been growing in an Erlenmeyer flask of Detmer  $\frac{1}{3}$  solution in diffuse light from a north window was poured over the agar in the petri dish. This suspension was allowed to remain on the agar for 24 hours; then the excess was removed. The petri-dish culture was placed in diffuse light from a north window until the surface of the agar was covered with a uniform green growth of algal cells. The glass plate covered with agar and algae was then cut out of the surrounding agar in the petri dish and placed upright in a sterilized closed brass container with a quartz window. A decker was arranged in front of the slit of the spectrograph to permit the exposure of three different portions of the plate for three different time periods.

Previous experimentation (Meier, 1934) has demonstrated that the wave lengths that prove lethal to the green cells of this alga do not affect the culture medium which covers the glass plate in any way that will accelerate or retard the subsequent growth of the algal cells.

The agar plates used in the experiments described here were inoculated September 6, 1934, and irradiated in October and November, as noted in table 1. Those plates irradiated in December were inoculated November 7. Previous experimentation (Meier, 1934) has shown that the difference in the age of the cultures has no apparent effect on the response of this alga to the ultraviolet irradiation.

A quartz mercury arc was used for irradiation of these cultures. The method of making the absolute measurements of the intensity of the lines in the ultraviolet spectrum with the vacuum thermocouple



and double monochromator is similar to the one described by Brackett and McAlister (1932).

### INTENSITY DATA

The intensity data for plates 39 to 57 are recorded in table 1. Intensities were measured with a thermocouple. The values to be given below represent the average intensities over the areas affecting the algae. A special experiment was planned to test the joint proportionality of the intensity of irradiation and the time of irradiation to

TABLE 1.—*Intensity Data*

Angstroms	October 26 Plates 39-45, intensity: ergs/sec. cm <sup>2</sup>	November 8 Plates 46-47, 50-52, intensity: ergs/sec. cm <sup>2</sup>	November 16 Plates 48, 49, 53, intensity: ergs/sec. cm <sup>2</sup>	December 12 Plates 54-57, intensity: ergs/sec. cm <sup>2</sup>
2250	200	280	297	297
2300	430	490	519	519
2323	220	220	233	233
2352	600	640	678	678
2378	940	1,050	1,110	1,110
2399	1,000	1,090	1,160	1,160
2447	320	330	350	350
2463	416	429	455	455
2483	2,340	2,400	2,540	2,540
2536	6,800	6,950	7,370	7,350
2576	535	640	678	678
2602	268	320	339	339
2652	5,900	6,100	6,420	6,730
2699	1,310	1,400	1,480	1,480
2753	960	960	1,020	1,020
2804	3,500	3,570	3,800	3,670
2894	1,500	1,620	1,720	1,720
2925	535	545	578	578
2967	4,300	4,250	4,510	4,510
3022	10,100	10,400	11,000	11,000
3130	20,200	20,300	21,500	21,500

the lethal effect. Accordingly, a smaller diaphragm was placed over the lens of the spectrograph so that five plates, plates 58-63, could be irradiated at  $\frac{1}{4}$  the original intensity, *i. e.*, the intensity used for irradiation of all the previous plates. By the adjustment of a 20-cm focal length lens in place of a 30-cm lens at the camera end of the spectrograph, a shorter, more intense spectrum was obtained, giving lines three times the intensity of the original spectrum. This very intense spectrum was used to irradiate plates 64-67. The intensity data for the  $\frac{1}{4}$  and 3-fold intensities are recorded in table 2, together with the original intensities of December 14.

## RESULTS

Decolorized cells appeared in the green plates where the wave lengths of ultraviolet proved to be lethal or radiotoxic. (See pl. 1.) The times of first appearance, *i. e.*, the periods elapsing between irradiation and visibility of the colorless regions, are tabulated for each plate in tables 3, 4, and 5. The exposure times are also shown in minutes and seconds.

TABLE 2.—*Relative Intensity Data*

Angstroms	Original intensity December 12 Plates 54-57, intensity: ergs/sec. cm <sup>2</sup>	$\frac{1}{2}$ original intensity December 12, 13 Plates 58-63, intensity: ergs/sec. cm <sup>2</sup>	$3 \times$ original intensity December 14 Plates 64-67, intensity: ergs/sec. cm <sup>2</sup>
2250	297	74	891
2300	519	130	1,557
2323	233	58	699
2352	678	170	2,034
2378	1,110	278	3,330
2399	1,160	289	3,480
2447	350	88	1,050
2463	455	114	1,365
2483	2,540	636	7,620
2536	7,350	1,838	22,050
2576	678	170	2,034
2602	339	85	1,017
2652	6,730	1,683	20,190
2699	1,480	371	4,440
2753	1,020	255	3,060
2804	3,670	916	11,010
2894	1,720	429	5,160
2925	578	145	1,734
2967	4,510	1,126	13,530
3022	11,000	2,756	33,000
3130	21,500	5,380	64,500

PROPORTIONALITY OF RADIOTOXICITY TO THE PRODUCT OF THE  
INTENSITY AND THE EXPOSURE TIME

In a previous paper (Meier, 1934) the assumption was made that the radiotoxic effect is proportional to the product of the intensity of irradiation and the duration of irradiation. In other words, a 3-minute exposure to  $x$  intensity should produce a given radiotoxic effect in the same reaction time as a 1-minute exposure to  $3x$  intensity; or again expressed differently, the reaction time is inversely proportional to the lethal dose, which is the product of the exposure time by the intensity.

To prove this assumption, experiments were performed with relative intensities of 1,  $\frac{1}{4}$ , and 3-fold, as shown in table 2. The results are recorded in tables 3, 4, and 5. As it is difficult to obtain algal plates coated precisely alike over the entire surface, some variation must be expected in observations of the reaction time or period between irradiation time and the first appearance of each radiotoxic region. Table 6 gives representative cases for each of the rays at the relative intensities studied. They show that for a range of 12-fold the proportionality holds within 40 or 50 percent in practically all cases and often much closer, thereby confirming the assumption that the lethal effect, as measured by the reciprocal of the reaction time, is proportional to the product of the exposure time and intensity. (See pl. 2.) As in many photochemical phenomena in the purely physical world, the total effect may depend on the total number of light quanta absorbed by the individual. If this is true, then any algal cell will die when the necessary number of quanta of ultraviolet irradiation have been absorbed.

#### THE LETHAL RADIOTOXIC THRESHOLD

A study of tables 1 and 3 indicates that the lethal radiotoxic threshold or minimum amount of radiotoxicity required to produce lethal effect for wave length 2250 Å lies at 720 seconds for an intensity of 280 ergs/sec.  $\text{cm}^2$ . Since the radiotoxic effect is proportional to the product of the intensity and the duration of irradiation, then for 1,000 ergs/sec.  $\text{cm}^2$  the exposure required for 2250 Å may be set as  $.280 \times 720 = 202$  seconds. The reciprocal of this threshold value, 202, gives the radiotoxic spectral sensitivity value, which, with the other computations given above, is recorded in table 7. For the sake of convenience the reciprocals are multiplied by 100. In a similar manner the radiotoxic spectral sensitivity value for each wave length was determined, as shown in table 7, and the smooth curve in figure 1 was drawn.

The determination of the lethal radiotoxic threshold factors as given in table 7 and the location of the radiotoxic spectral sensitivity value for each wave length in the radiotoxic spectral sensitivity curve in figure 1 are discussed in the following paragraphs.

2250 Å. No lethal region appeared for this wave length at the exposure of 600 seconds. The algae were killed by this ray in two plates at an exposure of 720 seconds, which gives a radiotoxic spectral sensitivity value of .495. The lethal regions, though visible, are not very distinct, and as the intensity of the ray is so small that multiplying by so large a factor as 3.6 gives a doubtful result, it does not seem



TABLE 3.—(Concluded)

Exposure min. time sec.	10 600	12 720		16 900		20 1,200		32 1,920	64 3,840
		46	47	46	47	46	47		
Plate no.	53								
Time of first appearance of radio-toxic regions	2 days	2 days	2 days	2 days	2 days	2 days	2 days	1 day	1 day
	2483	2300	2323	2300	2300	2300	2323	2300	2300
	2530	2323	2378	2323	2323	2323	2323	2323	2323
	2652	2652	2652	2378	2352	2352	2378	2352	2352
	2699	2699	2604	2652	2399	2378	2399	2378	2378
	2804	4 days	4 days	2804	2399	2399	2652	2399	2399
		2378	2300	4 days	2652	2447	2699	2483	2483
	3 days	2804	2300	4 days	2699	2447	2752	2530	2530
	2752	2570	2570	2447	2452	2570	2804	2852	2852
	2894	5 days	2602	2463	2652	2652	2804	2894	2894
		2483	2694	2463	2804	2804	2894	2894	2894
	8 days	2530	2483	2894	4 days	2894	4 days	2967	2967
	2570	2894	2530	2907	2300	2907	2300	2967	2967
	2602	2907	2570	2907	2447	2447	2447	2 days	2 days
			2483	5 days	2463	2463	2463	2 days	2 days
	19 days	7 days	2530	5 days	2378	2483	2483	2447	2447
	2378	2699	2699	2378	2378	2378	2378	2447	2447
	2399	2752	7 days	2483	2802	2802	2802	2447	2447
	2907	2752	2699	2530	2894	2602	2907	2447	2447
		27 days	2752	6 days	2967	2967	2967	2447	2447
		2250	2752	2399	5 days	7 days	5 days	2 days	2 days
		2602	2250	2399	2483	2600	2483	2 days	2 days
				7 days	2530	2752	2530	3 days	3 days
				2600	11 days	11 days	11 days	3 days	3 days
				2752	11 days	2250	2250	3 days	3 days
				3022	3022	3022	3022	6 days	6 days
				10 days	10 days	10 days	10 days	6 days	6 days
				3022	3022	3022	3022	6 days	6 days
				2250	2250	2250	2250	6 days	6 days
				3022	3022	3022	3022	6 days	6 days
				3022	3022	3022	3022	6 days	6 days

TABLE 4.—*Appearance of Radiotoxic Regions at  $\frac{1}{4}$  Original Intensity*

Exposure time	min. sec.	2	3	3½	4			6		14	16	56	64
		120	180	225	240			360		840	960	3,300	3,840
Plate no.		58, 59	59	58	58	59	60	60	61	60	61	62, 63	62, 63
Time of first appearance of radiotoxic regions		No lethal effect	8 days 2652 10 days 2530	8 days 2530 2652	8 days 2530 2652	6 days 2530 2652 35 days 2483 2804	5 days 2530 2652	5 days 2530 2652 6 days 2804	5 days 2530 2652 6 days 2804	5 days 2530 2652 6 days 2804	4 days 2483 2530 2652 6 days 2804	2 days 2378 2483 2530 2652 4 days 2804	2 days 2378 2483 2530 2652 4 days 2804



TABLE 5.—*Appearance of Radiotoxic Regions at 3 × Original Intensity*

Exposure time	min. sec.	30	2½ 150		64, 65		3½ 210		5 300	
Plate no.		64, 65	64, 65	66	67	64, 65	66	67	66	67
Time of first appearance of radiotoxic regions										
		5 days 2536 2652 2864	5 days 2536 2652 2864	4 days 2536 2652	4 days 2483 2536 2570	4 days 2536 2652 2864	4 days 2536 2652	4 days 2483 2536 2570	4 days 2536 2652 2864	4 days 2536 2652 2864
		25 days 2483 2699 2752	6 days 2483 2576 2699 2752	5 days 2483	4 days 2483 2699 2752 2894 2967	5 days 2483 2576 2699 2752	5 days 2483 2699 2752 2864	5 days 2483 2699 2752 2894 2967	5 days 2483 2699 2752	5 days 2483 2699 2752 2894 2967
			9 days 2894 2967	9 days 2894 2967		6 days 2483 2894	10 days 2894 2967		6 days 2576 2802 2804 2967	5 days 2894 2967
						8 days 2378 2399				5 days 2352
						9 days 2967				

TABLE 6.—*Proportionality of Radiotoxic Effect to Intensity and Irradiation Time*

A	Relative inten- sity	Plate no.	Expo- sure time, sec.	×	Inten- sity	×	Days	=	Prod- uct ÷ 10
2250	1	42	960		.200		6		115
	$\frac{1}{4}$	62	3,840		.074		4		114
2300	1	47	720		.490		4		141
	$\frac{1}{4}$	62	3,840		.130		4		200
2323	1	42	3,840		.220		1		845
	$\frac{1}{4}$	62	3,360		.058		4		780
	3	67	300		.699		4		839
2352	1	46	960		.640		5		307
	$\frac{1}{4}$	62	3,840		.170		4		261
	3	67	300		2.034		5		305
2378	1	41	480		.940		7		316
	$\frac{1}{4}$	62	3,840		.278		2		214
	3	67	300		3.330		4		400
2399	1	53	240		1.160		19		529
	$\frac{1}{4}$	62	3,840		.289		4		444
	3	67	300		3.480		4		418
2483	1	54	210		2.540		7		373
	$\frac{1}{4}$	62	3,840		.636		2		488
	3	67	150		7.620		4		457
2536	1	57	90		7.350		5		331
	$\frac{1}{4}$	59	180		1.838		10		331
	3	64	30		22.050		5		331
2576	1	41	240		.535		6		77.0
	$\frac{1}{4}$	60	840		.170		6		85.7
	3	67	150		2.034		4		122
2602	1	53	600		.339		8		163
	$\frac{1}{4}$	62	3,360		.085		7		200
	3	66	300		1.017		6		183
2652	1	57	50		6.730		8		269
	$\frac{1}{4}$	58	225		1.683		8		303
	3	64	30		20.190		5		303
2699	1	52	180		1.400		5		126
	$\frac{1}{4}$	60	840		.371		6		187
	3	67	150		4.440		4		266
2753	1	53	360		1.020		3		110
	$\frac{1}{4}$	60	840		.255		6		129
	3	67	150		3.060		4		184
2804	1	52	120		3.570		4		171
	$\frac{1}{4}$	61	360		.916		5		165
	3	64	30		11.010		5		165
2894	1	52	120		1.620		12		233
	$\frac{1}{4}$	60	840		.429		6		216
	3	67	150		5.160		4		310
2967	1	41	240		4.300		19		1961
	$\frac{1}{4}$	62	960		1.126		25		2702
	3	64	150		13.530		9		1825

that much weight should be given to this point. Therefore, in drawing the smooth curve, a questionable value of .380 is ascribed to this wave length.

TABLE 7.—*Lethal Radiotoxic Threshold and Radiotoxic Spectral Sensitivity*

A	Intensity ergs/sec. cm <sup>2</sup>	Lethal radiotoxic threshold For given intensity, sec.	For 1,000 ergs/sec. cm <sup>2</sup> , sec.	Radiotoxic spectral sensitivity Reciprocals × 100	Smooth curve
2250	280	720	202	.495	.380
2300	490	720	353	.283	
	490	650	319	.313	.313
2323	220	480	106	.943	
	699 <sup>a</sup>	300	210	.476	
	699	400	280	.357	.357
2352	600	480	288	.347	.404
2378	940	240	226	.442	.442
2399	1,000	240	240	.417	.417
2447	320	960	307	.326	.326
2463	416	960	399	.251	
	416	725	302	.331	
				.291 <sup>b</sup>	.300
2483	2,340	120	281	.356	
	2,540	165	419	.239	
				.298 <sup>c</sup>	.305
2536	7,350	40	294	.340	
	7,350	31	228	.439	.439
2576	678	240	163	.613	.613
2602	268	240	64	1.563	
	1,017 <sup>a</sup>	150	153	.654	.654
2652	6,730	40	269	.372	
	6,730	30	202	.495	.650
2699	1,310	120	157	.637	.625
2753	960	180	173	.578	.578
2804	3,570	60	214	.467	.505
2894	1,500	180	270	.370	.350
2925	535	1,920	1,027	.097	
	535	1,560	835	.120	.200
2967	4,300	240	1,032	.097	.097
3022	10,100	960	9,696	.010	.010
3130	20,200				

<sup>a</sup> See plate 67. <sup>b</sup> Mean of .251 and .331. <sup>c</sup> Mean of .356 and .239.

2300 A. No algae were killed at 2300 A by an exposure of 600 seconds. Lethal effect appears for the first time with one exposure at 720 seconds, which gives a radiotoxic spectral sensitivity value of .283. If it is assumed that there is lethal effect at 650 seconds' exposure, the lethal factor becomes .313.

2323 A. This ray produced a lethal effect with an exposure of 480 seconds, which gives a radiotoxic sensitivity value of .943. This value seems too high. In the 3-fold intensity experiment, 2323 A was lethal with 300 seconds' exposure on one plate, but not on any other plate, which would seem to indicate that the threshold is higher than 300 seconds. If an exposure time of 400 seconds is selected, a radiotoxic spectral sensitivity value of .357 is obtained.

2352 A. Algal cells were first killed by this ray at an exposure of 480 seconds, which gives a radiotoxic spectral sensitivity value of .347 and a value of .404 on the smooth curve.

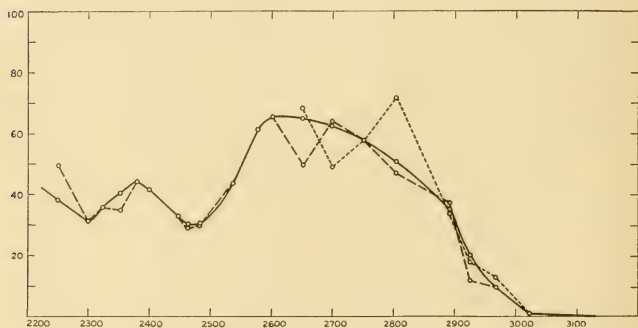


FIG. 1.—Radiotoxic spectral sensitivity of *Chlorella vulgaris* to ultraviolet rays. The abscissae are wave lengths in angstroms. The ordinates are relative lethal effectiveness in arbitrary units. Black line, smooth curve; dash line, actual values; dot line, curve obtained by Meier (1934).

2378 A. There was lethal action by this ray with an exposure of 240 seconds, which gives a radiotoxic spectral sensitivity value of .442.

2399 A. The lethal threshold of this ray is at 240 seconds' exposure, thus giving a radiotoxic spectral sensitivity value of .417.

2447 A. A lethal effect is first produced by this ray in the algal plates exposed for 960 seconds. The radiotoxic spectral sensitivity value is .326.

2463 A. On the algal plates, lethal effect was observed with an exposure of 960 seconds at two slightly different intensities, namely, 416 and 429 ergs/sec.  $\text{cm}^2$ . The lethal factor for 960 seconds at 416 ergs/sec.  $\text{cm}^2$  is .251. The exposure lower than 960 seconds was 720 seconds, and although there was no lethal effect on the algae at one 720-second exposure, it seems very possible, considering the intensity of the line, that there might be lethality at 725 seconds, thereby

raising the radiotoxic spectral sensitivity value to .331. The mean of these two values is .291, which gives a reasonable value of .300 on the smooth curve.

2483 Å. The algae were killed by this ray on two plates, but not on two others at 120 seconds' exposure, which would give a radiotoxic spectral sensitivity value of .356, which seems too high when plotted. At an exposure of 165 seconds and at higher exposures, the algae were always killed by this ray. If 165 seconds' exposure were considered as the threshold, the radiotoxic spectral sensitivity value would become .239, which seems too low in comparison with the intensity of the line. However, the mean of the two values seems reasonable, and on the smooth curve the point becomes .305.

2536 Å. This ray proved lethal at an exposure of 40 seconds, which gives a radiotoxic spectral sensitivity value of .340. There was no lethal effect with the 20 seconds' exposure, but as the intensity of the ray is very high, there possibly would have been lethal effect at 31 seconds, which gives a radiotoxic spectral sensitivity value of .439.

2576 Å. The lethal threshold for this wave length apparently lies at 240 seconds, which gives a radiotoxic spectral sensitivity value of .613. Lethal regions for this ray are perceived on one algal plate at 120 seconds' exposure, but not on five others; again on one plate at 180 seconds' exposure, but not on another at the same exposure; and there were no lethal regions on the three plates made at an exposure of 210 seconds. It is only at 240 seconds' exposure and higher that this lethal region appears with certainty.

2602 Å. If the exposure of 240 seconds is considered the lethal threshold of this ray, the radiotoxic spectral sensitivity value becomes 1.563, which is unreasonably high. In the experiment with 3-fold intensity the threshold is at 150 seconds, which gives a more reasonable radiotoxic spectral sensitivity value of .654.

2652 Å. The lethal threshold for this ray on the algal plates was 40 seconds, which gives a radiotoxic spectral sensitivity value of .372. Considering the high intensity of this ray, a very large divisor (6.7) was used to reduce it to the standard intensity of 1,000. Therefore this point has small weight and is probably too low. It is possible that lethal effect might have been produced at 30 seconds, since the 20 seconds' exposure showed no lethal effect. In that case the radiotoxic spectral sensitivity value would be .495, and .650 on the smooth curve.

2699 Å. 120 seconds' exposure to this ray produced lethal effects in four different plates, giving a radiotoxic spectral sensitivity value of .637, which is lowered to .625 on the smooth curve.

2753 A. This ray proved lethal to the algae in three plates at an exposure of 120 seconds, but no lethal regions for this ray appeared in the plates exposed for 165 seconds. Consequently, 180 seconds seems to mark the threshold of lethal action for 2753 A, thus giving a radiotoxic spectral sensitivity value of .578.

2804 A. An exposure of 60 seconds at an intensity of 3,570 ergs/sec.  $\text{cm}^2$  produced lethal action, whereas the same exposure at 3,500 ergs/sec.  $\text{cm}^2$  did not. Consequently, the first-named exposure seems to mark the threshold, giving a radiotoxic spectral sensitivity value of .467, which on the smooth curve becomes .505.

2894 A. Lethal regions for this ray first began to appear at an exposure of 120 seconds, but as they did not appear on the plates at an exposure of 165 seconds, the threshold seems to be in the vicinity of 180 seconds, which gives a radiotoxic spectral sensitivity value of .370, or .350 on the smooth curve.

2925 A. This ray, which is of very weak lethal value, did not kill the algae at an exposure of 1,200 seconds, but did at an exposure of 1,920 seconds, which would give it a radiotoxic spectral sensitivity value of .097. It seems more likely that the threshold would be midway between 1,200 and 1,920 seconds, or at 1,560 seconds, which would give a radiotoxic spectral sensitivity value of .120 or .200 on the smooth curve.

2967 A. The lethal threshold for this ray is at an exposure of 240 seconds, giving a radiotoxic spectral sensitivity value of .097.

3022 A. A lethal region for this ray is faintly visible at 960 seconds' exposure, thus giving a radiotoxic spectral sensitivity value of .010.

3130 A. This ray did not produce a lethal effect even in the experiment with 3-fold intensity.

The radiotoxic spectral sensitivity values of the curve previously determined by Meier (1934) when reduced to the same scale show reasonable agreement with the new values for the radio-toxic spectral sensitivity smooth curve as may be seen in figure 1.

#### RADIOTOXIC SPECTRAL SENSITIVITY AND RADIOTOXIC VIRULENCE

As described in a previous paper, the lethal response of the algae to the ultraviolet rays may be considered from two points of view: as to the radiotoxic spectral sensitivity and the radiotoxic virulence. The term "radiotoxic spectral sensitivity" relates to the certainty of the lethal action, while the term "radiotoxic virulence" may be used to describe the speed of the attack.

The determination of the radiotoxic spectral sensitivity, that is, the relative radiotoxicity of rays of different wave lengths when

applied with equal intensity and duration, has been measured as described in the preceding section. The determinations for each of the ultraviolet rays when plotted against wave lengths give a curve of radiotoxic spectral sensitivity. (See table 7 and fig. 1).

The radiotoxic virulence or the determination of the speed with which the toxic doses of the different rays produce lethal effects has been made by computing the brevity of time required to produce lethal effect for a standard radiotoxic quatum exceeding the lethal radiotoxic threshold.

A number of exposures in which many lethal wave length regions appeared were selected for determination of the radiotoxic virulence. The first appearances of these lethal regions were dispersed over long periods. The radiotoxic quatum, or the amount of radiotoxicity applied, is apparently proportional to (1) the exposure time, (2) the intensity of the ray, and (3) the radiotoxic spectral sensitivity. The radiotoxic virulence is, however, inversely proportional to (1) the radiotoxic quatum applied, and (2) the reaction time. Determinations of the virulence values for radiotoxic regions of 20 wave lengths with exposure times varying from 2 to 32 minutes were made as shown by the following example, which includes the computations for the wave length 2463 Å.

A	Plate no.	Exposure time, min.	× Inten- sity	× $\left\{ \begin{array}{l} \text{Radio-} \\ \text{toxic} \\ \text{spectral} \\ \text{sensi-} \\ \text{tivity} \end{array} \right\}$	$\left. \vphantom{\left\{ \begin{array}{l} \text{Radio-} \\ \text{toxic} \\ \text{spectral} \\ \text{sensi-} \\ \text{tivity} \end{array} \right\}} \right\} = \left\{ \begin{array}{l} \text{Radio-} \\ \text{toxic} \\ \text{quatum} \end{array} \right\}$	× Days =	Product	Reciprocals proportional to virulence
2463	42	16	4.16	3.00	199.8	3	599.4	.00167
	46	16	4.29	3.00	205.8	4	825.6	.00121
	47	16	4.29	3.00	205.8	4	825.6	.00121
	46	20	4.29	3.00	257.4	2	514.8	.00194
	47	20	4.29	3.00	257.4	4	1,029.6	.00097
	42	32	4.16	3.00	399.3	2	798.6	.00125

The virulence values for each exposure were then plotted against the wave lengths.

As the curve resulting from the 32-minute exposure on plate 42 included all 20 of the radiotoxic regions and appeared typical, it was chosen as a standard. The 12 other curves were then reduced to the same scale as the standard, 42 (32), in the following manner. First, each value of 42 (32) was divided by each corresponding value of the 12 other exposures. For example, the computations for 2463 Å would be:

Plate no. ....	42	42	46	47	46	47
Exposure time .....	32	16	16	16	20	20
2463 Å .....	1.00	0.75	1.03	1.03	0.64	1.29



The last preceding line results from dividing the numbers marked "reciprocals" above into .00125, the reciprocal corresponding to 42 (32).

In a similar manner the computations were made for all 20 wave lengths. After the widely divergent values had been discarded, the mean of all the values of each exposure was then determined, including all the observed wave lengths found on that exposure. This quantity is called "average multiplier" in the illustration below. Secondly, the products were found of each original virulence value multiplied by the corresponding mean value for each exposure, as shown below by continuing with the illustration of the wave length 2463 Å.

Plate no. ....	42	42	46	47	46	47		
Exposure time .....	32	16	16	16	20	20		
Average multiplier..	1.00	1.06	1.51	1.29	1.59	1.69	Sum	Virulence mean
2463 Å (x 100) ....	.125	.177	.183	.156	.308 <sup>a</sup>	.164	.805	.161

<sup>a</sup> This value, being wild, is rejected in the mean.

The mean for each wave length resulting from these final computations constitutes the general result of the whole research on virulence for each wave length, and each of the virulence values as plotted against the corresponding wave length gives the curve of radiotoxic virulence shown in figure 2.

The average deviation of the individual values of virulence from the mean was next determined in the following manner. As shown in the illustration given below, the difference of the final virulence mean from the individual mean value for each exposure of the individual wave lengths was computed.

Plate no. ....	42	42	46	47	46	47			
Exposure time .....	32	16	16	16	20	20	Average deviation	Average deviation percent	Probable error percent
2463 Å (deviation) .....	36	16	22	5	147 <sup>a</sup>	3	16.4	10.3	3.9

<sup>a</sup> This value, being wild, is rejected in the mean.

The mean of these differences for each wave length constitutes the average deviation. The percentage average deviation was then computed by dividing the average deviation for each wave length by the corresponding virulence mean. The percentage probable error was next computed according to the formula:

$$0.84 \text{ percentage average deviation} \\ \sqrt{n-1}$$

where  $n$  = the number of observations. The percentage probable error is illustrated in figure 2.



## DISCUSSION

The radiotoxic spectral sensitivity curve for the green alga *Chlorella vulgaris* in figure 1 is of the same general type in the region 2600 to 3130 Å as the curves representing bactericidal action and virus inactivation as found by Duggar and Hollaender (1934); the lethal effect on yeast by Oster (1934); the lethal effect on paramoecium by Weinstein (1930); and bactericidal action and protein coagulation by Sonne (1928), and Rivers and Gates (1928).

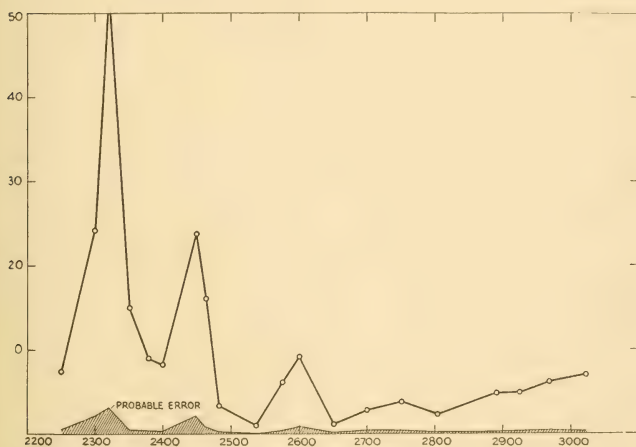


FIG. 2.—Radiotoxic virulence determined from *Chlorella vulgaris*. The abscissae are wave lengths in angstroms. The ordinates are radiotoxic virulence in arbitrary units.

Very little study has been made of the effect of wave lengths of the ultraviolet below 2600 Å on algae. Lucas (1934) has given us an idea of the actual effect of an ultraviolet ray on an individual algal cell. By means of a specially designed ultraviolet microscope with a monochromatic system, Lucas has photographed living cells of the blue-green alga *Gloecapsa*. Wave lengths 2573 Å and 2750 Å showed good definition of the cells, although the absorption of the cell increased at 2573 Å. At 2300 Å, the absorption of the cell was very strong, but the photographs were not sharp or distinct. No photographs were possible with wave length 2265 Å, as, for a second or two while under visible observation with the fluorescent ocular, the cells seemed agitated or strained and then suddenly increased to 5

or 10 times their original diameter. This distortion was followed by shrinkage and finally disintegration. Since wave length 2750 Å did not affect the cells, Lucas studied the reactions to wave length 2300 Å by photographing one specimen with wave length 2750 Å, irradiating it for a given time with wave length 2300 Å, and then rephotographing with wave length 2750 Å. By irradiating and photographing in regular sequence, Lucas obtained a series of photographs showing the cumulative effects of irradiation. At 2300 Å, the cells appeared quite opaque, and when the irradiation time was increased for this wave length, separation of the different cell parts occurred. At 2265 Å there was also general disintegration of the cells.

### SUMMARY

The radiotoxic spectral sensitivity of the unicellular green alga *Chlorella vulgaris* has been determined for 20 wave lengths in the ultraviolet ranging from 2250 Å to 3022 Å. As a preliminary step to facilitate deductions, an experiment was performed with three relative intensities which demonstrated that for a range of 12-fold the lethal effect as measured by the reciprocal of the reaction time is approximately proportional to the product of the exposure time and intensity. The results are in good accord with earlier observations as far as those went. They show maximum lethal sensitivity at about 2600 Å. The wave length 3130 Å, slightly longer than the short wave length limit of solar radiation reaching the earth's surface, had no lethal effect on the algal cells although of a greatly higher intensity than the toxic wave lengths. Since it is true that death ensued more quickly in some regions than in others, the radiotoxic virulence, or speed of effectiveness of each lethal ray in killing the algal cells for a radiotoxic quatum has been calculated for 20 wave lengths ranging from 2250 Å to 3022 Å. The results are of small percentage probable error, and they show an interesting wave of virulence alternately waxing and waning with decreasing wave length, but reaching a high maximum at 2323 Å.

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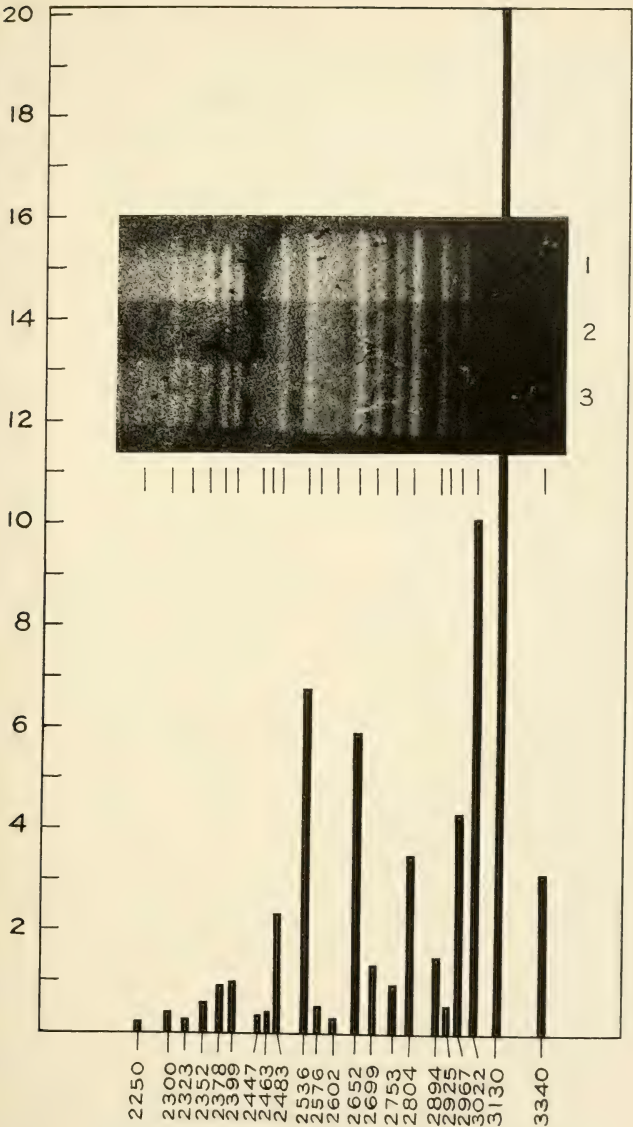
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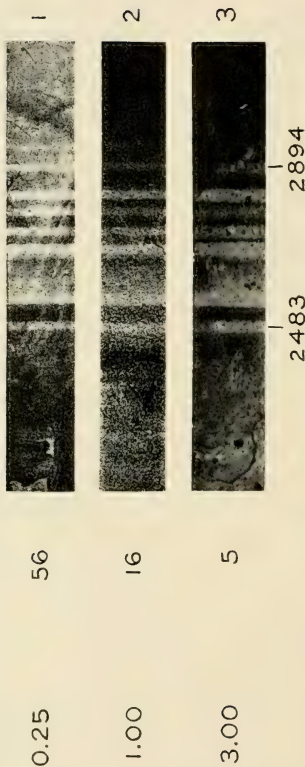


An algal spectrogram, obtained by exposing plate 42 of *Chlorella vulgaris* to ultraviolet rays for (1) 64 minutes, (2) 16 minutes, and (3) 32 minutes, superimposed on a diagram of the intensities of the wave lengths.

The abscissae are wave lengths in angstroms; the ordinates are intensities in thousands of ergs/sec.cm².

IRRADIATION  
TIME IN  
MINUTES

RELATIVE  
INTENSITY



Radiotoxic regions in (1) plate 62, (2) plate 42, (3) plate 67 of *Chlorella vulgaris* exposed to relative intensities of ultraviolet rays. The lethal regions on all three plates were visible about 4 days after irradiation.

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 3

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(WITH 11 PLATES)

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# LIQUID-PROPELLANT ROCKET DEVELOPMENT

BY ROBERT H. GODDARD

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(WITH 11 PLATES)

The following is a report made by the writer to the Daniel and Florence Guggenheim Foundation concerning the rocket development carried out under his direction in Roswell, N. Mex., from July 1930 to July 1932, and from September 1934 to September 1935, supported by this Foundation.

This report is a presentation of the general plan of attack on the problem of developing a sounding rocket, and of the results obtained. Further details will be set forth in a later paper, after the main objects of the research have been attained.

## INTRODUCTION

In a previous paper<sup>1</sup> the author developed a theory of rocket performance and made calculations regarding the heights that might reasonably be expected for a rocket having a high velocity of the ejected gases and a mass at all times small in proportion to the weight of propellant material. It was shown that these conditions would be satisfied by having a tapered nozzle through which the gaseous products of combustion were discharged,<sup>2</sup> by feeding successive portions of propellant material into the rocket combustion chambers,<sup>3</sup> and further by employing a series of rockets, of decreasing size, each fired when the rocket immediately below was empty of fuel.<sup>2</sup> Experimental results with powder rockets were also presented in this paper.

Since the above was published, work has been carried on for the purpose of making practical a plan of rocket propulsion set forth in 1914<sup>4</sup> which may be called the liquid-propellant type of rocket. In this rocket, a liquid fuel and a combustion-supporting liquid are fed under pressure into a combustion chamber provided with a conical nozzle through which the products of combustion are discharged.

<sup>1</sup> Smithsonian Misc. Coll., vol. 71, no. 2, 1919.

<sup>2</sup> U. S. Patent, Rocket Apparatus, No. 1,102,653, July 7, 1914.

<sup>3</sup> U. S. Patent, Rocket Apparatus, No. 1,103,593, July 14, 1914.

The advantages of the liquid-propellant rocket are that the propellant materials possess several times the energy of powders, per unit mass, and that moderate pressures may be employed, thus avoiding the weight of the strong combustion chambers that would be necessary if propulsion took place by successive explosions.

Experiments with liquid oxygen and various liquid hydrocarbons, including gasoline and liquid propane, as well as ether, were made during the writer's spare time from 1920 to 1922, under a grant by Clark University. Although oxygen and hydrogen, as earlier suggested,<sup>4</sup> possess the greatest heat energy per unit mass, it seems likely that liquid oxygen and liquid methane would afford the greatest heat value of the combinations which could be used without considerable difficulty. The most practical combination, however, appears to be liquid oxygen and gasoline.

In these experiments it was shown that a rocket chamber and nozzle, since termed a "rocket motor," could use liquid oxygen together with a liquid fuel, and could exert a lifting force without danger of explosion and without damage to the chamber and nozzle. These rockets were held by springs in a testing frame, and the liquids were forced into the chamber by the pressure of a noninflammable gas.

The experiments were continued from 1922 to 1930, chiefly under grants from the Smithsonian Institution. Although this work will be made the subject of a later report, it is desirable in the present paper to call attention to some of the results obtained. On November 1, 1923, a rocket motor operated in the testing frame, using liquid oxygen and gasoline, both supplied by pumps on the rocket.

In December 1925 the simpler plan previously employed of having the liquids fed to the chamber under the pressure of an inert gas in a tank on the rocket was again employed, and the rocket developed by means of these tests was constructed so that it could be operated independently of the testing frame.

The first flight of a liquid oxygen-gasoline rocket was obtained on March 16, 1926, in Auburn, Mass., and was reported to the Smithsonian Institution May 5, 1926. This rocket is shown in the frame from which it was fired, in plate 1, figure 1. Pressure was produced initially by an outside pressure tank, and after launching by an alcohol heater on the rocket.

It will be seen from the photograph that the combustion chamber and nozzle were located forward of the remainder of the rocket, to which connection was made by two pipes. This plan was of advantage

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<sup>4</sup> Smithsonian Misc. Coll., vol. 71, no. 2, 1919.

in keeping the flame away from the tanks, but was of no value in producing stabilization. This is evident from the fact that the direction of the propelling force lay along the axis of the rocket, and not in the direction in which it was intended the rocket should travel, the condition therefore being the same as that in which the chamber is at the rear of the rocket. The case is altogether different from pulling an object upward by a force which is constantly vertical, when stability depends merely on having the force applied above the center of gravity.

Plate 1, figure 2 shows an assistant igniting the rocket, and plate 2, figure 1 shows the group that witnessed the flight, except for the camera operator. The rocket traveled a distance of 184 feet in 2.5 seconds, as timed by a stop watch, making the speed along the trajectory about 60 miles per hour.

Other short flights of liquid oxygen-gasoline rockets were made in Auburn, that of July 17, 1929, happening to attract public attention owing to a report from someone who witnessed the flight from a distance and mistook the rocket for a flaming airplane. In this flight the rocket carried a small barometer and a camera, both of which were retrieved intact after the flight (pl. 2, fig. 2). The combustion chamber was located at the rear of the rocket, which is, incidentally, the best location, inasmuch as no part of the rocket is in the high velocity stream of ejected gases, and none of the gases are directed at an angle with the rocket axis.

During the college year 1929-30 tests were carried on at Fort Devens, Mass., on a location which was kindly placed at the disposal of the writer by the War Department. Progress was made, however, with difficulty, chiefly owing to transportation conditions in the winter.

At about this time Col. Charles A. Lindbergh became interested in the work and brought the matter to the attention of the late Daniel Guggenheim. The latter made a grant which permitted the research to be continued under ideal conditions, namely, in eastern New Mexico; and Clark University at the same time granted the writer leave of absence. An additional grant was made by the Carnegie Institution of Washington to help in getting established.

It was decided that the development should be carried on for 2 years, at the end of which time a grant making possible 2 further years' work would be made if an advisory committee, formed at the time the grant was made, should decide that this was justified by the results obtained during the first 2 years. This advisory committee

was as follows: Dr. John C. Merriam, chairman; Dr. C. G. Abbot; Dr. Walter S. Adams; Dr. Wallace W. Atwood; Col. Henry Breckinridge; Dr. John A. Fleming; Col. Charles A. Lindbergh; Dr. C. F. Marvin; and Dr. Robert A. Millikan.

#### THE ESTABLISHMENT IN NEW MEXICO

Although much of the eastern part of New Mexico appeared to be suitable country for flights because of clear air, few storms, moderate winds, and level terrain, it was decided to locate in Roswell, where power and transportation facilities were available.

A shop 30 by 55 feet was erected in September 1930 (pl. 3, figs. 1, 2), and the 60-foot tower previously used in Auburn and Fort Devens was erected about 15 miles away (pl. 4, fig. 1). A second tower, 20 feet high (pl. 4, fig. 2), was built near the shop for static tests, that is, those in which the rocket was prevented from rising by heavy weights, so that the lift and general performance could be studied. These static tests may be thought of as "idling" the rocket motor. A cement gas deflector was constructed under each tower, as may be seen in plate 4, figures 1, 2, whereby the gases from the rocket were directed toward the rear, thus avoiding a cloud of dust which might otherwise hide the rocket during a test.

#### STATIC TESTS OF 1930-32

Although, as has been stated, combustion chambers had been constructed at Clark University which operated satisfactorily, it appeared desirable to conduct a series of thorough tests in which the operating conditions were varied, the lift being recorded as a function of the time. Various modifications in the manner of feeding the liquids under pressure to the combustion chamber were tested, as well as variations in the proportions of the liquids, and in the size and shape of the chambers. The chief conclusions reached were that satisfactory operation of the combustion chambers could be obtained with considerable variation of conditions, and that larger chambers afforded better operation than those of smaller size.

As will be seen from plate 4, figure 2, the supporting frame for the rocket was held down by four steel barrels containing water. Either two or four barrels could be filled, and in the latter case the total weight was about 2,000 lbs. This weight was supported by a strong compression spring, which made possible the recording of the lift on a revolving drum (pl. 5, fig. 1) driven by clockwork.

The combustion chamber finally decided upon for use in flights was  $5\frac{3}{4}$  inches in diameter and weighed 5 pounds. The maximum lift obtained was 289 pounds, and the period of combustion usually exceeded 20 seconds. The lifting force was found to be very steady, the variation of lift being within 5 percent.

The masses of liquids used during the lifting period were the quantities most difficult to determine. Using the largest likely value of the total mass of liquids ejected and the integral of the lift-time curve obtained mechanically, the velocity of the ejected gases was estimated to be over 5,000 feet per second. This gave for the mechanical horsepower of the jet 1,030 hp., and the horsepower per pound of the combustion chamber, considered as a rocket motor, 206 hp. It was found possible to use the chambers repeatedly.

The results of this part of the development were very important, for a rocket to reach great heights can obviously not be made unless a combustion chamber, or rocket motor, can be constructed that is both extremely light and can be used without danger of burning through or exploding.

#### FLIGHTS DURING THE PERIOD 1930-32

The first flight obtained during this period was on December 30, 1930, with a rocket 11 feet long, weighing 33.5 pounds. The height obtained was 2,000 feet, and the maximum speed was about 500 miles per hour. A gas pressure tank was used on the rocket to force the liquid oxygen and the gasoline into the combustion chamber.

In further flights pressure was obtained by gas pressure on the rocket, and also by pumping liquid nitrogen through a vaporizer, the latter means first being employed in a flight on April 19, 1932.

In order to avoid accident, a remote control system was constructed in September 1931, whereby the operator and observers could be stationed 1,000 feet from the tower, and the rocket fired and released at will from this point. This arrangement has proved very satisfactory. Plate 5, figure 2 shows the cable being unwound between the tower and the 1,000-foot shelter, the latter being seen in the distance, and plate 6, figure 1 shows the control keys being operated at the shelter, which is provided with sand bags on the roof as protection against possible accident. Plate 5, figure 2 shows also the level and open nature of the country.

One observer was stationed 3,000 feet from the tower, in the rear of the 1,000-foot shelter, with a recording telescope (pl. 6, fig. 2). Two pencils attached to this telescope gave a record of the altitude and azimuth, respectively, of the rocket, the records being made on a paper



strip, moved at a constant speed by clockwork. The sights at the front and rear of the telescope, similar to those on a rifle, were used in following the rocket when the speed was high. In plate 7, figure 1, which shows the clock mechanism in detail, the observer is indicating the altitude trace. This device proved satisfactory except when the trajectory of the rocket was in the plane of the tower and the telescope. For great heights, short-wave radio direction finders, for following the rocket during the descent, will be preferable to telescopes.

During this period a number of flights were made for the purpose of testing the regulation of the nitrogen gas pressure. A beginning on the problem of automatically stabilized vertical flight was also made, and the first flight with gyroscopically controlled vanes was obtained on April 19, 1932, with the same model that employed the first liquid nitrogen tank. The method of stabilization consisted in forcing vanes into the blast of the rocket<sup>3</sup> by means of gas pressure, this pressure being controlled by a small gyroscope.

As has been found by later tests, the vanes used in the flight of April 19, 1932, were too small to produce sufficiently rapid correction. Nevertheless, the two vanes which, by entering the rocket blast, should have moved the rocket back to the vertical position were found to be warmer than the others after the rocket landed.

This part of the development work, being for the purpose of obtaining satisfactory and reproducible performance of the rocket in the air, was conducted without any special attempt to secure great lightness, and therefore great altitudes.

In May 1932 the results that had been obtained were placed before the advisory committee, which voted to recommend the 2 additional years of the development. Owing to the economic conditions then existing, however, it was found impossible to continue the flights in New Mexico.

A grant from the Smithsonian Institution enabled the writer, who resumed full-time teaching in Clark University in the fall of 1932, to carry out tests that did not require flights, in the physics laboratories of the University during 1932-33, and a grant was received from the Daniel and Florence Guggenheim Foundation which made possible a more extended program of the same nature in 1933-34.

#### RESUMPTION OF FLIGHTS IN NEW MEXICO

A grant made by the Daniel and Florence Guggenheim Foundation in August 1934, together with leave of absence for the writer granted

<sup>3</sup> U. S. Patent, Mechanism for Directing Flight, No. 1,879,187, September 27, 1932.



by the Trustees of Clark University, made it possible to continue the development on a scale permitting actual flights to be made. This was very desirable, as further laboratory work could not be carried out effectively without flights in which to test performance under practical conditions.

Work was begun in September 1934, the shop being put in running order and the equipment at the tower for the flights being re-

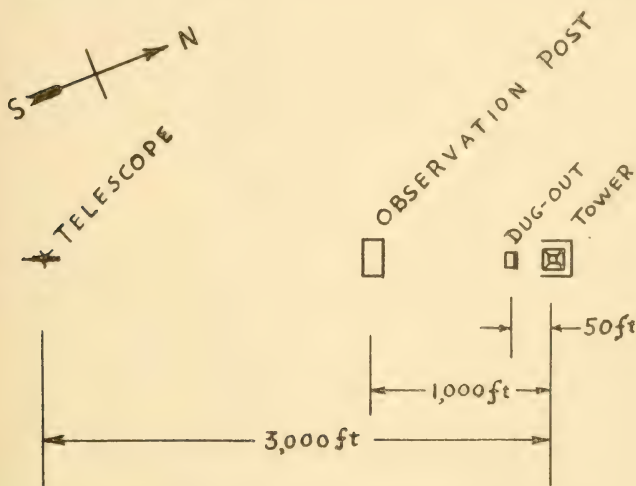


FIG. 1.—Relative positions of launching tower, dugout, shelter, and telescope.

placed. The system of remote control previously used was further improved and simplified, and a concrete dugout (pl. 7, fig. 2) was constructed 50 feet from the launching tower in order to make it possible for an observer to watch the launching of the rocket at close range. The relative positions of launching tower, dugout, shelter, and telescope are shown in figure 1.

#### DEVELOPMENT OF STABILIZED FLIGHT

It was of the first importance to perfect the means of keeping the rockets in a vertical course automatically, work on which was begun in the preceding series of flights, since a rocket cannot rise vertically to a very great height without a correction being made when it deviates from the vertical course. Such correction is especially important at the time the rocket starts to rise, for a rocket of very great range

must be loaded with a maximum amount of propellant and consequently must start with as small an acceleration as possible. At these small initial velocities fixed air vanes, especially those of large size, are worse than useless, as they increase the deviations due to the wind. It should be remarked that fixed air vanes should preferably be small, or dispensed with entirely, if automatic stabilization is employed, to minimize air resistance.

In order to make the construction of the rockets as rapid as possible, combustion chambers were used of the same size as those in the work of 1930-32, together with the simplest means of supplying pressure, namely, the use of a tank of compressed nitrogen gas on the rocket. The rockets were, at the same time, made as nearly streamline as possible without resorting to special means for forming the jacket or casing.

#### PENDULUM STABILIZER

A pendulum stabilizer was used in the first of the new series of flights to test the directing vanes, for the reason that such a stabilizer could be more easily constructed and repaired than a gyroscope stabilizer, and would require very little adjustment. A pendulum stabilizer could correct the flight for the first few hundred feet, where the acceleration is small, but it would not be satisfactory where the acceleration is large, since the axis of the pendulum extends in a direction which is the resultant of the acceleration of the rocket and the acceleration of gravity, and is therefore inclined from the vertical as soon as the rocket ceases to move in a vertical direction. The pendulum stabilizer, as was expected, gave an indication of operating the vanes for the first few hundred feet, but not thereafter. The rocket rose about 1,000 feet, continued in a horizontal direction for a time, and finally landed 11,000 feet from the tower, traveling at a velocity of over 700 miles per hour near the end of the period of propulsion, as observed with the recording telescope.

#### GYROSCOPE STABILIZER

Inasmuch as control by a small gyroscope is the best as well as the lightest means of operating the directing vanes, the action of the gyroscope being independent of the direction and acceleration of the rocket, a gyroscope having the necessary characteristics was developed, after numerous tests.

The gyroscope, shown in plate 8, figure 1, was set to apply controlling force when the axis of the rocket deviated  $10^{\circ}$  or more from the vertical. In the first flight of the present series of tests with gyro-

scopic control, on March 28, 1935, the rocket as viewed from the 1,000-foot shelter traveled first to the left and then to the right, thereafter describing a smooth and rather flat trajectory. This result was encouraging, as it indicated the presence of an actual stabilizing force of sufficient magnitude to turn the rocket back to a vertical course. The greatest height in this flight was 4,800 feet, the horizontal distance 13,000 feet, and the maximum speed 550 miles per hour.

In subsequent flights, with adjustments and improvements in the stabilizing arrangements, the rockets have been stabilized up to the time propulsion ceased, the trajectory being a smooth curve beyond this point. In the rockets so far used, the vanes have moved only during the period of propulsion, but with a continuation of the supply of compressed gas the vanes could evidently act against the slip stream of air as long as the rocket was in motion in air of appreciable density. The oscillations each side of the vertical varied from  $10^{\circ}$  to  $30^{\circ}$  and occupied from 1 to 2 seconds. Inasmuch as the rockets started slowly, the first few hundred feet of the flight reminded one of a fish swimming in a vertical direction. The gyroscope and directing vanes were tested carefully before each flight, by inclining and rotating the rocket while it was suspended from the 20-foot tower (pl. 8, fig. 2). The rocket is shown in the launching tower, ready for a flight, in the close-up (pl. 9, fig. 1), and also in plate 9, figure 2, which shows the entire tower.

The behavior of the rocket in stabilized flight is shown in plates 10 and 11, which are enlarged from 16-mm motion picture films of the flights. The time intervals are 1.0 second for the first 5 seconds, and 0.5 second thereafter. The 60-foot tower from which the rockets rise (pl. 9, fig. 2) appears small in the first few of each set of the motion pictures, since the camera was 1,000 feet away, at the shelter shown in plate 6, figure 1. The continually increasing speed of the rockets, with the accompanying steady roar, make the flights very impressive. In the two flights for which the moving pictures are shown, the rocket left a smoke trail and had a small, intensely white flame issuing from the nozzle, which at times nearly disappeared with no decrease in roar or propelling force. This smoke may be avoided by varying the proportion of the fluids used in the rocket, but is of advantage in following the path of the rocket. The occasional white flashes below the rocket, seen in the photographs, are explosions of gasoline vapor in the air.

Plate 10 shows the flight of October 14, 1935, in which the rocket rose 4,000 feet, and plate 11 shows the flight of May 31, 1935, in which the rocket rose 7,500 feet. The oscillations from side to side,

above mentioned, are evident in the two sets of photographs. These photographs also show the slow rise of the rocket from the launching tower, but do not show the very great increase in speed that takes place a few seconds after leaving the tower, for the reason that the motion picture camera followed the rockets in flight.

A lengthwise quadrant of the rocket casing was painted red in order to show to what extent rotation about the long axis occurred in flight. Such rotation as was observed was always slow, being at the rate of 20 to 60 seconds for one rotation.

As in the flights of 1930-32 to study rocket performance in the air, no attempt was made in the flights of 1934-35 to reduce the weight of the rockets, which varied from 58 to 85 pounds. A reduction of weight would be useless before a vertical course of the rocket could be maintained automatically. The speed of 700 miles per hour, although high, was not as much as could be obtained by a light rocket, and the heights, also, were much less than could be obtained by a light rocket of the same power.

It is worth mentioning that inasmuch as the delicate directional apparatus functioned while the rockets were in flight, it should be possible to carry recording instruments on the rocket without damage or changes in adjustment.

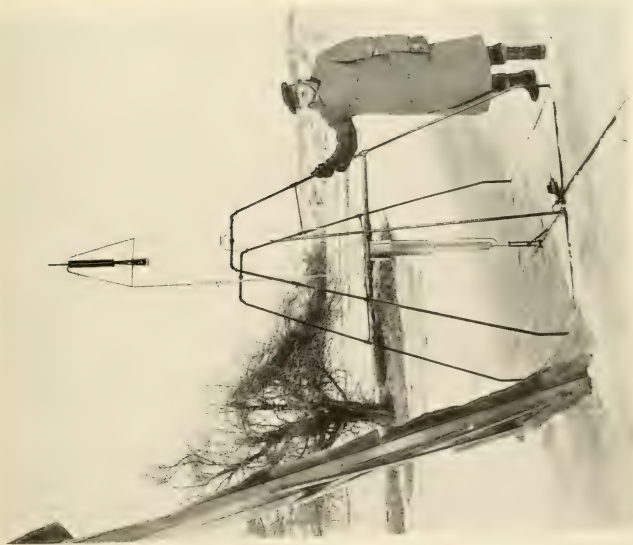
#### FURTHER DEVELOPMENT

The next step in the development of the liquid-propellant rocket is the reduction of weight to a minimum. Some progress along this line has already been made. This work, when completed, will be made the subject of a later report.

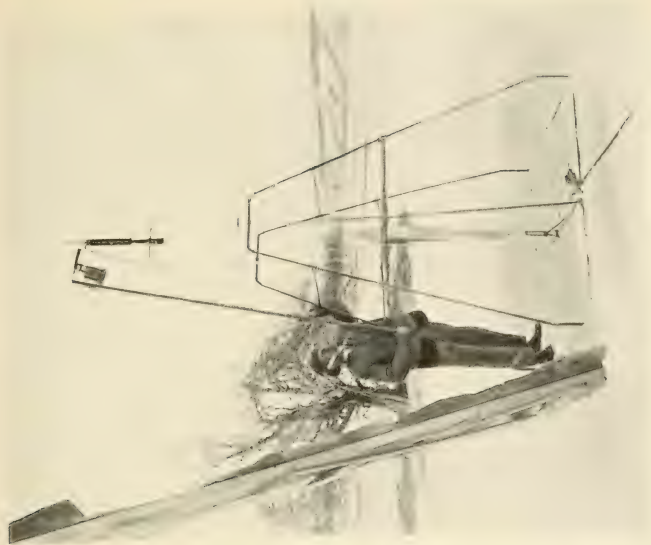
#### CONCLUSION

The chief accomplishments to date are the development of a combustion chamber, or rocket motor, that is extremely light and powerful and can be used repeatedly, and of a means of stabilization that operates automatically while the rocket is in flight.

I wish to express my deep appreciation for the grants from Daniel Guggenheim, the Daniel and Florence Guggenheim Foundation, and the Carnegie Institution of Washington, which have made this work possible, and to President Atwood and the Trustees of Clark University for leave of absence. I wish also to express my indebtedness to Dr. John C. Merriam and the members of the advisory committee, especially to Col. Charles A. Lindbergh for his active interest in the work and to Dr. Charles G. Abbot, Secretary of the Smithsonian Institution, for his help in the early stages of the development and his continued interest.



1. Liquid oxygen-gasoline rocket in the frame from which it was fired on March 16, 1926, in Auburn, Mass.

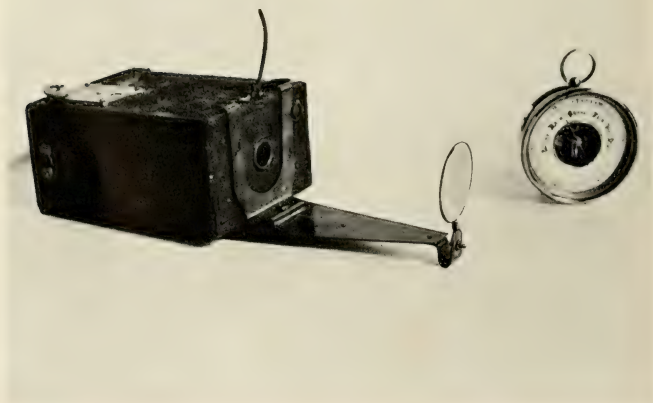


2. Assistant igniting the rocket shown in figure 1.





1. Group that witnessed the flight of the rocket shown in plate 1.



2. Barometer and camera retrieved intact after the flight of July 17, 1929.



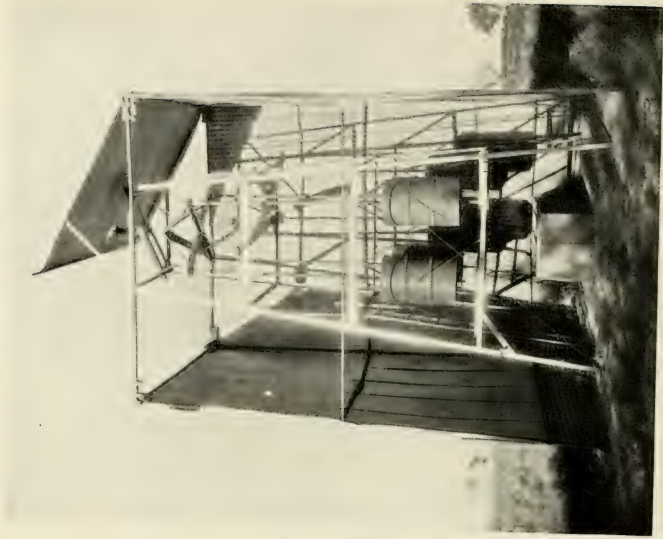
1. Shop erected at Roswell, N. Mex., in September 1930.



2. Interior of shop.

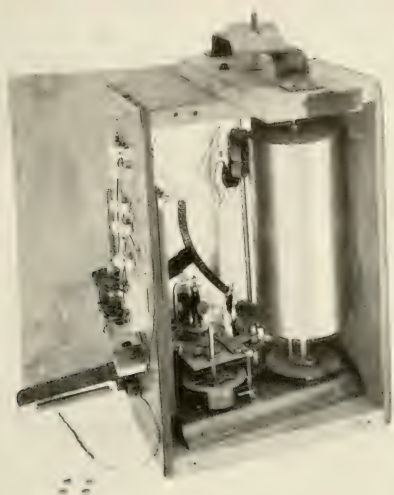


1. 60-foot tower, previously used in Auburn and Fort Devens, as erected at Roswell, N. Mex.



2. 20-foot tower for static tests at Roswell, N. Mex.





1. Revolving drum to record the lift developed in static tests in the 20-foot tower.



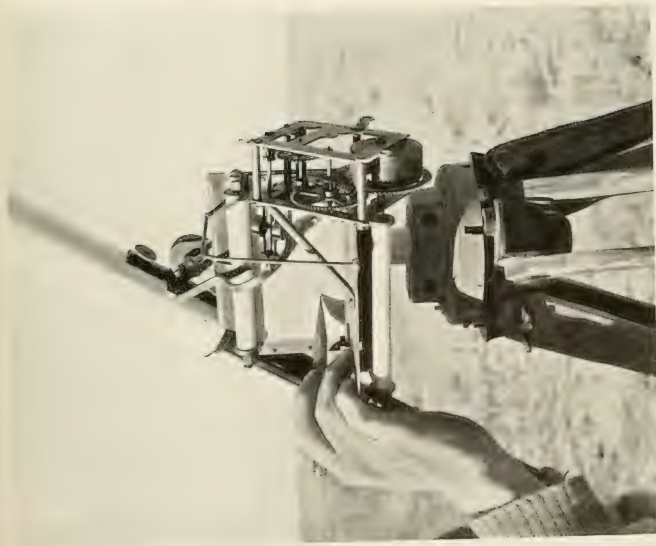
2. Cable being unwound between the tower and the 1,000-foot shelter.



1. Control keys being operated at the shelter.



2. Observer stationed 3,000 feet from the tower with a recording telescope.



1. Clock mechanism on the recording telescope; the observer is indicating the altitude trace.



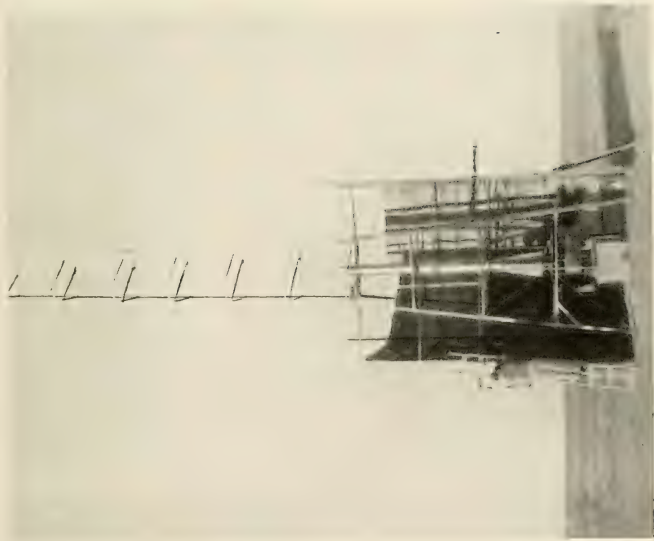
2. Concrete dugout constructed 50 feet from the launching tower so that an observer can watch the launching of the rocket at close range.



1. The gyroscope stabilizer.



2. Testing the gyroscope and directing vanes before a flight by inclining and rotating the rocket while it was suspended from the 20-foot tower.



1. Rocket in the launching tower, ready for a flight.



2. Same as figure 1, except that the entire tower is shown.



O



1



2



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4



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5.5

6

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7

7.5

8

8.5

9



9.5



10



10.5

91



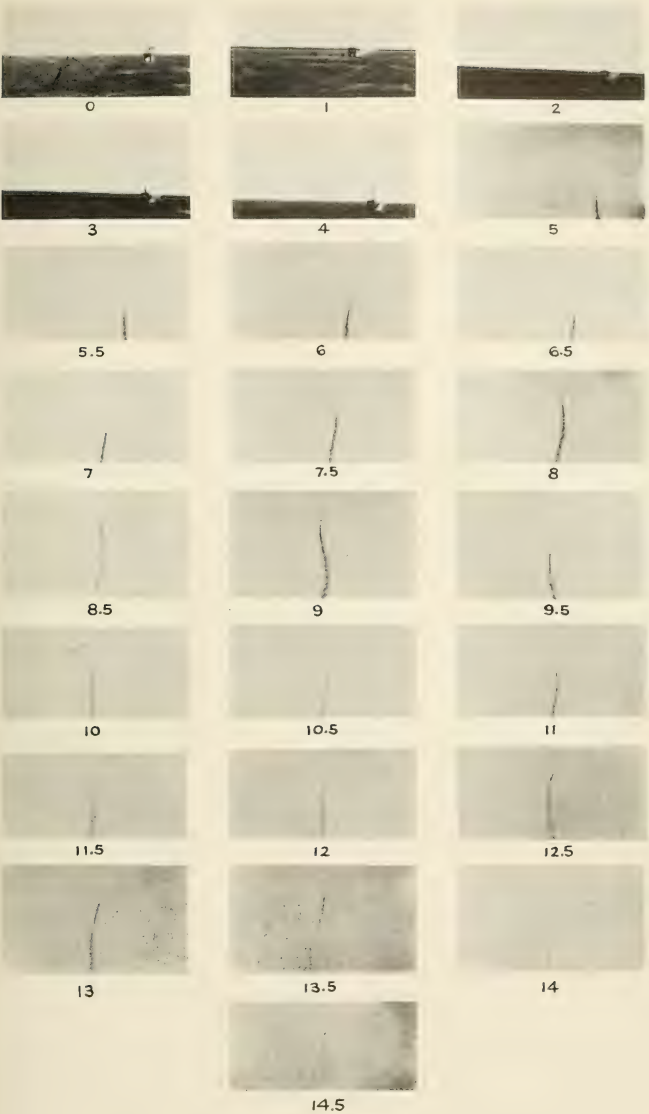
11.5

12

TIME IN SECONDS

The flight of October 14, 1935, in which the rocket rose 4,000 feet.





TIME IN SECONDS

The flight of May 31, 1935, in which the rocket rose 7,500 feet.





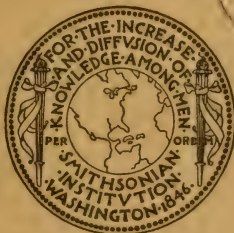
SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 95, NUMBER 4

SECOND CONTRIBUTION  
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BY

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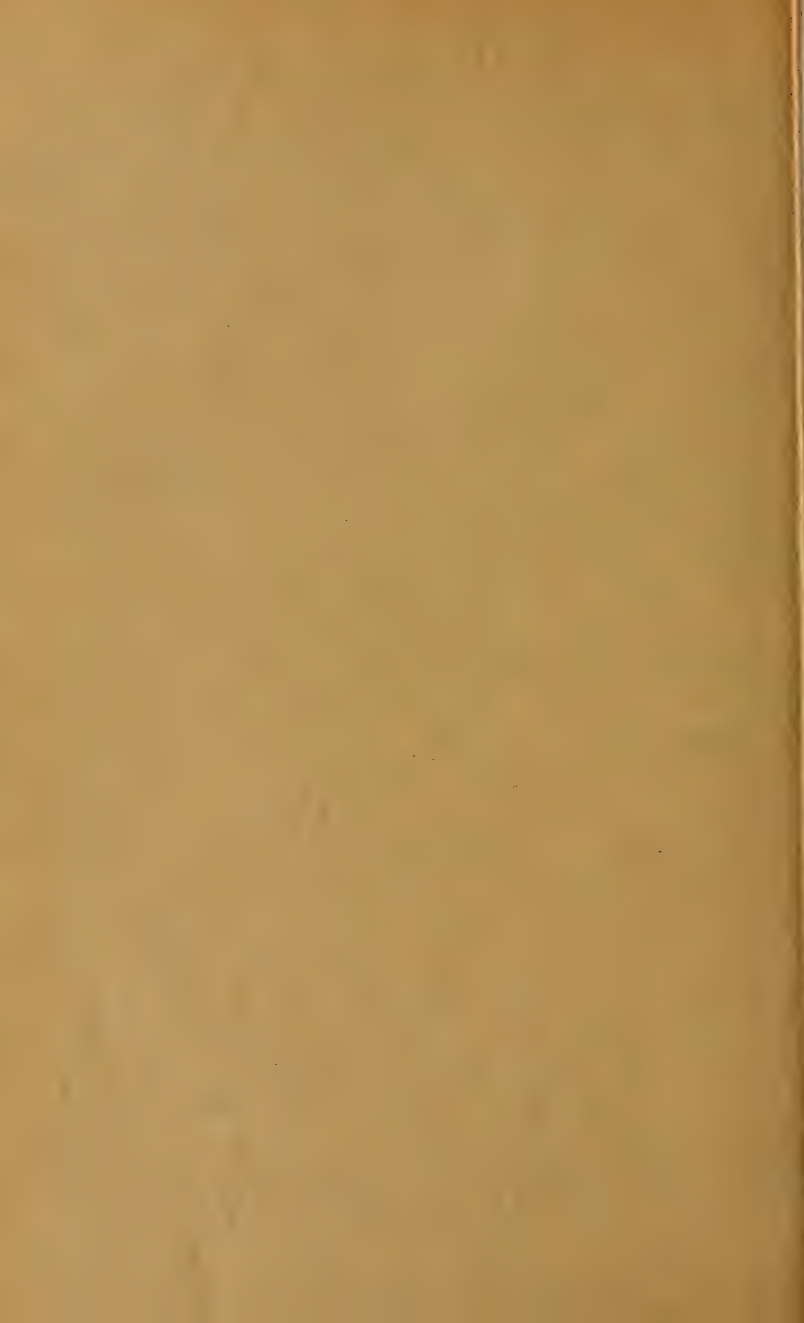
Curator, Division of Invertebrate Paleontology,  
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(PUBLICATION 3383)



CITY OF WASHINGTON  
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## SECOND CONTRIBUTION TO NOMENCLATURE OF CAMBRIAN TRILOBITES

By CHARLES ELMER RESSER

Curator, Division of Invertebrate Paleontology  
U. S. National Museum

This is the second paper in a series dealing with nomenclatural changes necessary for certain Cambrian species.<sup>1</sup> In this contribution several Atlantic Province genera and species are discussed.

As in the previous paper, only published species are considered because illustrations are not possible. Most of the text is arranged in alphabetical order according to genera, exceptions being made in a few cases where several members of a family are kept together.

### ALBERTELLA Walcott, 1908

Four species were described by Walcott as belonging to *Albertella*, viz, the genotype *A. helena*, and *A. bosworthi*, *A. levis*, and *A. pacifica*. The last named, which comes from Asia, is in reality an indeterminate fragment and must await the finding of further material before its proper generic assignment can be made. Several new species of *Albertella* are in hand beside those recognized below in the discussion of the three previously described American species.

Previous mention has not been made in the literature of the close relationship between *Albertella* and *Ptarmingia*. In fact, this is another case where the cranidia of the two genera are indistinguishable generically.

#### *Albertella helena* Walcott

#### Genotype

*Albertella helena* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 19, pl. 2, figs. 1-4, 1908. (Not 5 = *Ptarmingia gordonensis*; 6 = *A. similis*; 7 = *A. rossensis*; 8, 9 = *A. nitida*.) Idem, vol. 67, no. 2, p. 39, pl. 7, fig. 4, 1917.

Middle Cambrian, Gordon; (loc. 5j) near Scapegoat Mountain, and (loc. 4o) Gordon Creek, Powell County, Montana.

<sup>1</sup>Resser, Charles Elmer, Nomenclature of some Cambrian trilobites, Smithsonian Misc. Coll., vol. 93, no. 5, Feb. 14, 1935.

*Lectotype*.—U.S.N.M. no. 53410; paratypes, nos. 53407, 53409, 53411, 53412.

***Albertella bosworthi* Walcott**

*Albertella bosworthi* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 22, pl. 1, figs. 4, 5, 1908. (Not 6 = *A. similis*; 7 = *A. nitida*). Idem, vol. 67, no. 2, p. 38, pl. 7, figs. 3a, 3b, 1917. (Not 2-2b = *A. robsone*; 3, 3c = *A. similis*; 3d = *A. nitida*.)

Much confusion exists among the illustrated specimens assigned to this species because the wide and narrow forms and those in which there is a macropleural development of the fourth or the third thoracic segment were not noted.

Middle Cambrian, Ptarmigan; (locs. 35c, 18a, 63m) Mount Bosworth, and (loc. 63j) Popes Peak, above Ross Lake, British Columbia.

*Lectotype*.—U.S.N.M. no. 53416; paratypes, nos. 53413, 63763; plesiotypes, no. 85221.

***Albertella similis*, n. sp.**

*Albertella bosworthi* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 22, pl. 1, fig. 6; pl. 2, fig. 6, 1908; idem, vol. 67, no. 2, pl. 7, figs. 3, 3c, 1917 (see *A. bosworthi*).

*Albertella helena* WALCOTT (part), idem, vol. 53, no. 2, p. 19, pl. 2, fig. 6, 1908.

This species is close to *A. bosworthi*, differing chiefly in its longer pleura, wider pygidium, and striated free cheeks.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 63762; paratypes, nos. 53414, 53415, 53417.

***Albertella rossensis*, n. sp.**

*Albertella helena* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 19, pl. 2, fig. 7, 1908 (see *A. helena*).

This species is similar to *A. helena* in shape and in the macropleural development of the third segment, but differs in having coarser granules and in lacking both the axial spines on the pygidium and the short interpleural furrows.

Occurrence same as preceding.

*Holotype and paratypes*.—U.S.N.M. no. 53403.

***Albertella nitida*, n. sp.**

*Albertella bosworthi* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 22, pl. 1, fig. 7, 1908. Idem, vol. 67, no. 2, p. 38, pl. 7, fig. 3d, 1917 (see *A. bosworthi*).

*Albertella helena* WALCOTT (part), idem, pl. 2, figs. 8, 9, 1908; idem, vol. 67, no. 2, p. 39, pl. 7, figs. 5, 5a, 1917 (see *A. helena*).



This is a rather small form characterized by long, slender pleural and pygidial spines, with a macroleural development of the last thoracic segment.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 63766; paratypes, nos. 53402, 53404, 53405, 53406, 63764, 63765.

***Albertella robsonensis*, n. sp.**

*Albertella bosworthi* WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 2, p. 38, pl. 7, figs. 2-2b, 1917 (see *A. bosworthi*).

The glabella is long and somewhat more expanded than in the more southern species. The pygidium reflects the same characteristic in its narrowness and long, narrow, prominent axis. Its pleural lobes are very flat, even when compared with *A. similis*.

Middle Cambrian, Chetang; (loc. 61p) Coleman Creek, and (loc. 61w) Terrace Creek, Robson Park, Alberta.

*Cotypes*.—U.S.N.M. nos. 63759-63761.

**AMECEPHALINA Poulsen, 1927**

***Amecephalina convexa* (Walcott)**

*Anomocare convexa* WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 4, p. 87, pl. 17, figs. 2-2d, 1911; Research in China, vol. 3, Carnegie Inst. Publ. 54, p. 187, pl. 18, figs. 3-3c, 1913.

Middle Cambrian, Conasauga; (loc. 90x) 3 miles east of Center, Alabama.

*Lectotype*.—U.S.N.M. no. 57597; paratypes, nos. 57595, 57596.

**ANTAGMUS, n. gen.**

For many years certain common Lower Cambrian trilobites were referred to various genera, depending on the genus to which the author was comparing them at the moment, or on a particular feature which attracted his attention. Some revision is now possible, but until this genus and its related forms can be studied thoroughly, any suggested realignment of the species must be tentative.

*Diagnosis*.—Cranidium rather wide and convex in both directions; facial suture diverging anterior to the eyes. Glabella well defined, tapering, about two-thirds the length of the cranidium, with two or three pairs of short glabellar furrows. Brim consists almost entirely of a rim, usually somewhat thickened and particularly characterized by its increased width in the middle, which is due to the backward course of the anterior furrow to meet the dorsal furrow in front of the cranidium.

Available species indicate 15 thoracic segments. These specimens also indicate that the genus had a rather simple and relatively small pygidium in which the dorsal furrow only is well defined.

*Comparisons.*—Comparisons should be made with *Kochiella* and its allies, the chief distinguishing features being the convexity and reduction in the brim.

*Genotype.*—*Ptychoparia teucer* Walcott.

*Name.*—*avraw* = meet; *ογμος* = furrow.

*Range.*—Lower Cambrian of the Appalachians and Cordilleran regions.

**Antagmus teucer (Walcott) not Billings**

*Ptychoparia teucer* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 197, pl. 26, fig. 3, 1886; 10th Ann. Rep. U. S. Geol. Surv., p. 652, pl. 96, fig. 3, 1891.

Lower Cambrian, Winooski; (loc. 25a) 1½ miles east of Swanton, Vermont.

*Holotype.*—U.S.N.M. no. 15436.

**ARMONIA Walcott, 1924**

*Armonia* WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 54, 1924; idem, no. 3, p. 69, 1925.

Confusion of species led to description of the genotype under two specific and generic names. Consequently, the genotype for *Armonia* must rest on the older name.

This genus, like many others, is difficult to determine without whole specimens, for the cranidium of *Armonia* is not easily distinguished from that of *Blainia* or even *Asaphiscus*. However, the respective pygidia differ so much that the retention of the several genera is warranted.

*Diagnosis.*—Trilobite as a whole ovate. Cephalon semicircular. Glabella wide, tapered, nearly three-fourths the length of the head. Posterolateral limbs wide, blunt. Suture anterior to eyes, which are situated about the middle of the head, diverges moderately; intramarginal for some distance. Glabellar furrows faintly indicated; occipital furrow strong.

Thorax with about 14 segments; bluntly terminated.

Pygidium somewhat triangular with a tendency toward extension laterally of the anterior corners. Axis well defined, extending almost to the rear margin. Pleural lobes well marked by both the pleural furrows and grooves which extend practically to the margin.

*Comparisons.*—Comparing *Armonia elongata* with *Blainia gregaria*, it will be noted that the glabella of *Armonia* is somewhat longer and

the rim flatter. Also the thorax is somewhat longer, but the chief difference is in the pygidium. *Armonia* has a transverse pygidium, whereas that of *Blainia* is almost quadrate and moreover is more convex. Further comparisons will appear in the discussion of other similar genera.

*Genotype*.—*Asaphiscus* (*Blainia*) *elongatus* Walcott (part).

*Range*.—Middle Cambrian of the southern Appalachians.

#### ***Armonia elongata* (Walcott)**

*Asaphiscus* (*Blainia*) *elongatus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 393, pl. 63, figs. 4, 4a, 1916. (Pygidium represents another genus.)

*Armonia pelops* WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 54, pl. 10, fig. 1, 1924; idem, no. 3, p. 69, pl. 17, figs. 28-31, 1925.

When the specimens contained in the chert cobbles were first described, an incorrect pygidium was chosen. Later when the same species occurring in the dark shales containing the nodules was described, new generic and specific names were used.

Middle Cambrian, Conasauga (Rogersville equivalent); (locs. 90x, 95, 92) southeast of Center, Cherokee County, Alabama.

*Lectotype*.—U.S.N.M. no. 62812; paratypes, no. 62811; plesiotypes, nos. 72276-72279.

#### **BONNASPIS, n. gen.**

The Middle Cambrian species from Mount Stephen, British Columbia, on which Walcott evidently planned to base his genus *Karlia*, does not belong to *Corynexochus*, of which *Karlia minor* is a good species. In consequence *K. stephenensis* becomes the type of a new genus for which the name *Bonnaspis* seems appropriate, inasmuch as a relationship with *Bonnia* is evident.

*Diagnosis*.—Small trilobites oval in shape, with subequal head and tail shields. Glabella of moderate size, expanded forward, with faint furrows. Eyes small, situated at the midpoint. Fixed cheeks moderately wide, with eye lines.

Free cheeks narrow with long and heavy genal spines.

Thorax with seven segments; pleura bluntly terminated.

Pygidium wider than distance between eyes, semicircular, well fused, with axial and pleural furrows shallow. Pleural furrows extend to margin.

*Genotype*.—*Karlia stephenensis* Walcott.

*Range*.—Rare in the Middle Cambrian of British Columbia.

*Comparisons*.—Comparing *Bonnaspis* with *Bonnia*, the outstanding distinction is the expansion of the glabella and the apparent absence of

marginal spines at the anterior angles of the pygidium. Were this a Lower Cambrian form, it is doubtful that a separate genus would be recognized because in *Bonnia senecta* (Billings) and several undescribed species considerable expansion of the glabella takes place.

***Bonnaspis stephenensis* (Walcott)**

*Menocephalus salteri*? ROMINGER (not Devine), Proc. Acad. Nat. Sci., Philadelphia, pt. 1, p. 16, pl. 1, fig. 6, 1887.

*Karlia stephenensis* WALCOTT, Proc. U. S. Nat. Mus., vol. 11, p. 445, 1888; Canadian Alpine Journ., vol. 1, pt. 2, p. 224, pl. 3, fig. 4, 1908; Smithsonian Misc. Coll., vol. 64, no. 3, p. 224, pl. 36, fig. 8, 1916.

*Corynexochus ræmingeri* MATTHEW, Trans. Roy. Soc. Canada, 2d ser., vol. 5, sec. 4, p. 47, pl. 2, fig. 3, 1899.

*Corynexochus stephenensis* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 324, pl. 55, figs. 5-5e, 1916.

Middle Cambrian, Stephen; (loc. 14s) Mount Stephen, above Field, British Columbia.

*Holotype*—U.S.N.M. no. 61731; paratypes, nos. 62717, 62718.

**BONNIA Walcott, 1916**

*Corynexochus* (*Bonnia*) WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 325, 1916.

*Bonnia* RAYMOND, Amer. Journ. Sci., 5th ser., vol. 15, no. 88, p. 309, 1928.

*Bonnia* was proposed as a subgenus of *Corynexochus* Angelin, but it is doubtful whether the two genera can remain in the same family. American species were rather carelessly assigned to the two genera, a relic of the earlier days of paleontology when it was customary to locate an existing genus to receive new forms.

Walcott made *Bathyrurus parvulus* Billings the genotype but based his description on specimens from Bonne Bay, which represent several considerably different species. Moreover, hitherto the *Bonnia* species have been studied from a small fraction of available specimens picked out of a tray because they happened to break free of the matrix. This resulted in description of only a fraction of the species represented in this very prolific trilobite genus.

The National Museum of Canada kindly lent the specimens marked as Billings' types, which presumably are the ones restudied by Matthew. Without access to these specimens it would have been impossible to determine exactly what the described species are. Unfortunately Billings' type specimens were not marked by him, and consequently in this case it is not possible to go back of Matthew's 1897 paper, except to distinguish between the specimens available in 1861 and those subsequently collected in 1872 by T. C. Weston, which, of course, could

not have been studied by Billings before his report was published. Fortunately, the two species recognized by Billings are clearly distinguishable among the several species represented by the types sent from Ottawa.

*Diagnosis*.—Small trilobites characterized by a long and essentially quadrate glabella. Glabella usually quadrate, but sometimes expanded forward; occupying the entire length of the cranidium. Glabellar furrows usually very faint. Brim confined to a narrow concave rim. Fixed cheeks about equal to width of glabella. Eyes rather large, extending somewhat forward of the middle of the head, eye lines present. Free cheeks small, generally with short genal spines.

Pygidium about the same size as cranidium. Segments fused; pleural furrows usually well defined. Axis usually well above level of pleural lobes. One to three marginal spines occur at anterior angles.

*Genotype*.—*Bathyurus parvulus* Billings.

*Range*.—Lower Cambrian, North America and Asia.

Species of *Bonnia* not discussed in this paper include: *B. groenlandica* Poulsen, *B. busa* Walcott, *B. breunus* Walcott, and *B. fieldensis* Walcott.

#### ***Bonnia parvula* (Billings)**

*Bathyurus parvulus* BILLINGS, Pal. Foss., Geol. Surv. Canada, pt. 1, p. 16, fig. 21, November 1861.

*Bathyurus senectus* BILLINGS (part), idem, fig. 20 (fig. 19 = *B. senecta*).

*Bathyurus senectus* MATTHEW (part), Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 196, pl. 4, fig. 4b, 1897 (figs. 4, 4a = *B. senecta*).

*Dorypyge parvula angifrons* MATTHEW, idem, p. 197, pl. 4, figs. 6, 6a, 1897.

It has been difficult to clear up the confusion of species grouped under the few named forms of *Bonnia*, but with Billings' and Walcott's types in hand solution of the problem is possible. The foregoing synonymy shows how this was accomplished for *B. parvula*, by confining the species to specimens from Labrador available to Matthew in 1897. Inasmuch as *Dorypyge parvula* and Matthew's variety *angifrons* are quite distinct species, an effort was made to retain both names, but since the same specimen was evidently used as the type for both, they must be regarded as synonyms, and a new name must be given to Matthew's *B. parvula*. This conclusion is inescapable when the original labels are read, for they state that the specimen to which Matthew gave the varietal name was collected by Richardson in 1861, whereas the other specimens identified by Billings and figured by Matthew as *D. parvula* were collected by T. C. Weston in 1872. Therefore, Billings' name must be restricted to the fossils he had available when he described his species in 1861. Moreover, applica-

tion of a drop of acid to Billings' holotype causes it to effervesce freely, showing that its brown fine-grained appearance misled Matthew into calling the rock a sandstone and in consequence suggesting Vermont as the possible locality. In fact, Richardson, the collector, was also misled by this appearance, for the original label reads "grey sandstone."

All other specimens, including Walcott's identifications, referred in literature to *B. parvula*, represent new species.

As to the pygidium, Matthew describes none for this species, but both he and Billings figure a pygidium with *B. senecta*, which may be no. 433a of the Billings types available, and which by its features matches the holotype cranidium. Moreover, the matrix has the same peculiar brown sandstone appearance in contrast to the lighter, more crystalline limestone in which the other specimens are preserved.

*B. parvula* is characterized by its parallel-sided glabella, the absence of glabellar furrows, in short, by simplicity in all its features.

Lower Cambrian, Forteau; L'Anse au Loup, Labrador.

*Holotype*.—Nat. Mus. Canada no. 433; plesiotype, no. 433a.

***Bonnia matthewi*, n. sp.**

*Dorypyge parvula* MATTHEW (not Billings), Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 197, pl. 4, figs. 5-5c, 1897.

*Corynexochus (Bonnia) parvulus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 328, pl. 57, figs. 1, 1b, 1c, 1916.

As explained in the discussion of *B. parvula*, these specimens came into the collections in 1872 and were then identified with Billings' species described in 1861. Matthew's description of *B. parvula* is based on this head and tail, which he illustrates.

*Comparisons*.—Compared with *B. parvula* this species is much wider. The glabella expands slightly forward, and the rim is both flatter and wider. Moreover, the pygidium is very distinct, owing to its broad rim, to the reduction of the pleural ribs to narrow sloping ridges, and to the larger marginal spines. Above all, the presence of lines on all elevated portions of the test serves to distinguish the species from all others present in Labrador.

Occurrence same as preceding.

*Cotypes*.—Nat. Mus. Canada nos. 427, 433g.

***Bonnia senecta* (Billings)**

*Bathyrus senectus* BILLINGS (part), Pal. Foss., Geol. Surv. Canada, pt. 1, p. 15, fig. 19, November 1861 (see *B. parvula*).

*Bathyriscus senectus* MATTHEW (part), Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 196, pl. 4, figs. 4, 4a, 1897 (see *B. parvula*).



Billings' description and illustration are inadequate to identify the species. Subsequently, Matthew restudied the type preserved at Ottawa, concluding that it is not the holotype but a specimen substituted by Billings for it. However, since the figures of both authors clearly indicate a form with expanded glabella, and since this specimen is the only such form among the types, it may be regarded as Matthew's neoholotype.

All specimens from other localities identified as *B. senecta* belong to other species. Those illustrated by Walcott in 1916 from Bonne Bay and Quebec must be studied with the great number of new species in hand from those localities before they can be placed in their proper species.

*Comparisons*.:—Comparing *B. senecta* with the other species in Labrador, it is at once distinguished by its long, expanding glabella, the rather strong glabellar furrows, and the rounded frontal outline.

Occurrence same as preceding.

*Neoholotype*.—Nat. Mus. Canada no. 420.

***Bonnia columbensis*, n. sp.**

*Corynexochus* (*Bonnia*) *senectus* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 319, pl. 55, figs. 7-7c, 1916.

Compared with *B. senecta*, this species is very simple. Its outstanding characteristic is the rounded lines in all its parts. Fusion is carried far in the pygidium.

Lower Cambrian, Mount Whyte; (loc. 61d) southwest slope of Mount Shaffer, British Columbia.

*Lectotype*.—U.S.N.M. no. 62722; paratypes, nos. 62723-62725.

***Bonnia clavata* (Walcott)**

*Ptychoparia?* (Subgenus?) *clavata* WALCOTT, Amer. Journ. Sci., 3d ser., vol. 34, p. 198, pl. 1, fig. 3, 1887.

*Corynexochus clavatus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 316, pl. 55, fig. 4, 1916 (not fig. 4b = *B. salemensis*; fig. 4a is a worthless composite drawing).

This is a very small trilobite, and the specimens include at least two species. In the first place the composite drawing used in 1887 and subsequently repeated in 1891 and 1916, must be discarded both because it is incorrectly drawn and because it is based on at least two species. Further, figure 4 of the 1916 paper, which is the holotype of the species, needs correction. Carefully made enlarged photographs show no more trace of glabellar furrows than the smooth glabella indicates under a lens. In addition this head is crushed so that the expansion of the glabella is somewhat accentuated. With allowance for this



distortion, the species still has a glabella that expands somewhat more than the extreme in other species, but it does not seem to be enough more to warrant the establishment of a new genus.

Lower Cambrian, Schodack; 2 miles south of North Granville, New York.

*Holotype*.—U.S.N.M. no. 17454a.

**Bonnia salemensis, n. sp.**

*Corynexochus clavatus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 316, pl. 55, fig. 4b, 1916 (see *B. clavata*).

This form has strong glabellar furrows, exceeding in this respect as well as in length of glabella the similar features in *B. senecta*.

Lower Cambrian, Schodack; (loc. 43a) 1 mile northeast of Salem, New York.

*Holotype*.—U.S.N.M. no. 17454b.

**Bonnia bubaris (Walcott)**

*Corynexochus bubaris* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 314, pl. 56, fig. 2, 1916. (Not fig. 2a = *B. bicensis*; 2b = *B. quebecensis*; figs. 3, 3a = *B. wanneri*; figs. 3b-3f = *B. tumifrons*.)

Lower Cambrian; (loc. 2 o) boulders, Bic, Quebec.

*Holotype*.—U.S.N.M. no. 62734.

**Bonnia bicensis, n. sp.**

*Corynexochus bubaris* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 314, pl. 56, fig. 2a (only), 1916 (see *B. bubaris*).

This species differs from *B. bubaris* in its greater and more even convexity, longitudinally.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 62735.

**Bonnia quebecensis, n. sp.**

*Corynexochus bubaris* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 314, pl. 56, fig. 2b (only), 1916 (see *B. bubaris*).

Coarse lined surface ornamentation distinguishes this form from *B. bubaris*.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 62736.

**Bonnia wanneri, n. sp.**

*Corynexochus bubaris* WALCOTT (part), Smithsonian Misc. Coll. vol. 64, no. 5, p. 314, pl. 56, figs. 3, 3a, 1916 (see *B. bubaris*).

Compared with *B. bubaris*, this species is not only larger but lacks glabellar furrows and in side view is seen to be arched only in its anterior third.

Lower Cambrian, Kinzers; (loc. 49) near Emigsville, north of York, Pennsylvania.

*Holotype*.—U.S.N.M. no. 62737; paratype, no. 62738.

***Bonnia tumifrons*, n. sp.**

*Corynexochus bubaris* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 314, pl. 56, figs. 3b-3f, 1916 (see *B. bubaris*).

This is a very distinct species characterized by the shortness, width, and great convexity of its glabella, the presence of glabellar furrows, the blunt thoracic segments and the presence of three lateral spines on the pygidium.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 62739; paratypes, nos. 62740-72743.

***Bonnia capito* (Walcott)**

*Corynexochus capito* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 315, pl. 57, figs. 2, 2a, 1916. (Not 2b = *B. lata*; 2c = *B. swantonensis*; 2d-e = *B. vermontensis*.)

This species must be confined to the York locality.

Lower Cambrian, Kinzers; (loc. 48b) York, Pennsylvania.

*Cotypes*.—U.S.N.M. nos. 62746-62747.

***Bonnia lata*, n. sp.**

*Protypus senectus* WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 213, pl. 31, fig. 2 (only), 1886 (figs. 2a-c = *B. swantonensis*); 10th Ann. Rep. U. S. Geol. Surv., p. 655, pl. 98, fig. 7 (only), 1891.

*Corynexochus capito* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 315, pl. 57, fig. 2b (only), 1916 (see *B. capito*).

A similarly wide but relatively longer form as compared with *B. tumifrons*.

Lower Cambrian, Parker; (locality stated to be loc. 25), Parker Quarry, Georgia, Vermont, but the material suggests Swanton.

*Holotype*.—U.S.N.M. no. 15421a.

***Bonnia swantonensis*, n. sp.**

*Corynexochus capito* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 315, pl. 57, fig. 2c (only), 1916 (see *B. capito*).

A small smooth species with a slightly expanded glabella.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 15421b.

***Bonnia vermontensis*, n. sp.**

*Protypus senectus* WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 213, pl. 31, figs. 2a-c (only), 1886 (see *B. capito*); 10th Ann. Rep. U. S. Geol. Surv., p. 655, pl. 98, figs. 7a-c (only), 1891.

*Corynexochus capito* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 5, p. 315, pl. 57, figs. 2d, e (only), 1916 (see *B. capito*).

Compared with *B. lata* this is a narrow form and finer also in its other features.

Occurrence same as preceding.

*Cotypes*.—U.S.N.M. no. 15421c, d.

**CEDARIA** Walcott, 1924

***Cedaria burnetensis* (Walcott)**

*Ptychoparia burnetensis* WALCOTT, Proc. U. S. Nat. Mus., vol. 13, p. 272, pl. 21, fig. 1, 1890.

Two cranidia and a pygidium occur on the single small block containing the holotype.

Upper Cambrian, Hickory; (loc. 67x) Tatur Hill, Burnet County, Texas.

*Holotype*.—U.S.N.M. no. 23854.

**CLAVASPIDELLA** Poulsen, 1927

***Clavaspidella sylla* (Walcott)**

*Bathyriscus (Poliella) sylla* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 354, pl. 48, figs. 3-3f, 1916.

*Clavaspidella sylla* RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 21, 1935.

The references to this and the following species were mixed in typing the 1935 report.

Middle Cambrian, Chetang; (loc. 61 o) Coleman Glacier Creek, 7 miles northeast of Robson Peak, Alberta.

*Lectotype*.—U.S.N.M. no. 62645; paratypes, nos. 62646-62651.

***Clavaspidella probus* (Walcott)**

*Bathyriscus (Poliella) probus* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 354, pl. 65, figs. 2, 2a, 1916.

It will be noted that this is the youngest species referred to the genus. Moreover, in several features it is no longer fully typical, and for this reason some question concerning its generic affinities must remain.

Middle Cambrian, Marjum; (loc. 11 o) about 4 miles southeast of Antelope Springs, House Range, Utah.

*Cotypes*.—U.S.N.M. no. 62837, 62838.

**CONOCORYPHIDAE** Angelin, 1878

The trilobite species referred to this family need thorough revision, but to do the task properly would require a monographic study of several years duration. However, a hasty review of the literature permits a tentative revision of the group which seems to warrant publica-

tion. Even though all bibliographic references are at hand, which offers an advantage previous students of the group did not have, nevertheless the usual difficulties of working without specimens—with only descriptions and drawings—renders some of the following decisions of doubtful value.

Each described genus is discussed and its validity judged as far as the information available permits. Previous workers often considered chiefly local material, and sometimes the rules of nomenclature were not kept in mind. Therefore, it is hoped that the following discussion will shorten the labors of the person who will monograph this interesting group of trilobites.

*Diagnosis.*—Eyeless trilobites of ordinary size. Glabella well defined, tapered, with short recurved pairs of furrows. Genal spines usually lacking. Surface granulated or lined, or both. Equivalent of eye lines usually present. Thorax with about 15 segments; pleura blunt. Pygidium small, well fused, with well-impressed dorsal furrow and pleural grooves.

The family is evidently confined to the Middle Cambrian of the Atlantic Province, with three Asiatic incursions.

Synonyms of the various species are listed under the genera to which they were last referred by competent students, but a list of the genera regarded as valid follows. All species which appear referable to the family, with two exceptions, can be cared for by using existing genera.

*Conocoryphe* Corda, 1847

*Ctenocephalus* Corda, 1847

*Bailiella* Matthew, 1885

*Bailiaspis*, new genus

*Holocephalina* Salter, 1864

*Dasometopus*, new genus

*Hartshillia* Illing, 1915

*Liocephalus* Grönwall is evidently a synonym of *Holocephalina*, and *Hartella* is eliminated as a synonym of *Ctenocephalus*.

#### CONOCORYPHE Corda, 1847

*Conocoryphe* CORDA, Abh. k. bömischen Gesell. Wiss., vol. 5, p. 139, 1847.

*Conocoryphe* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 103, 1885.

*Conocoryphe* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, pp. 82, 84, 213, 1902.

The foregoing bibliography includes only those references which contribute to the understanding of this and related genera. Species belonging to many other families have been referred to *Conocoryphe*, as well as those representing other genera within the family.

*Diagnosis.*—Eyeless trilobite, oval in outline. Glabella tapered, with several sets of short, recurved furrows; extends nearly to the anterior

furrow. Deep marginal furrow extends all around the cephalon, being interrupted only at the genal angles. Two short diverging furrows cross the preglabellar area, joining the dorsal with the marginal furrow, thus making a distinct lobe anterior to the glabella. Eye ridges faint.

Thorax of 15 segments, with blunt tips. Pygidium fused, transverse.

*Comparisons.*—Since *Conocoryphe* is the type of family, comparisons of the other genera will be made with it.

*Genotype.*—*Trilobites sulzeri* Schlotheim.

*Range.*—Middle Cambrian of the Atlantic Province, associated with *Paradoxides*.

Species formerly referred to *Conocoryphe* are now referred as follows:

- |   |   |
|---|---|
| <i>C. abdita</i> Salter = <i>Conocephalina</i>                          | <i>C. homfrayi</i> Hicks = <i>Ptychoparia</i>                                     |
| <i>C. adamsi</i> Miller = <i>Ptychoparella</i>                          | <i>C. humerosa</i> Salter = <i>Conocoryphe</i> ?                                  |
| <i>C. aequalis</i> Linnarsson = <i>Bailiella</i>                        | <i>C. impressa</i> Linnarsson = <i>Bailiella</i>                                  |
| <i>C. applanata</i> Salter = <i>Solenopleura</i>                        | <i>C. invita</i> Salter = <i>Conocephalina</i>                                    |
| <i>C. baileyi</i> Hartt = <i>Bailiella</i>                              | <i>C. kingii</i> = <i>Elrathia</i>  |
| <i>C. brachymetopus</i> Linnarsson =<br><i>Solenopleura</i>             | <i>C. lantenoisi</i> Mansuy = <i>Bailiella</i>                                    |
| <i>C. breviceps</i> = <i>Dasometopus</i>                                | <i>C. laticeps</i> Angelin = <i>Ctenocephalus</i>                                 |
| <i>C. bucephala</i> Belt = <i>Beltella</i>                              | <i>C. latifrons</i> Corda = <i>Conocoryphe</i>                                    |
| <i>C. bufo</i> Hicks = <i>Bailiaspis</i>                                | <i>C. levyi</i> Munier-Chalmas and<br>Bergeron = <i>Bailiella</i>                 |
| <i>C. bullata</i> Howell = <i>Bailiella</i>                             | <i>C. ? longispinus</i> Belt = <i>Olenus</i>                                      |
| <i>C. coronata</i> Barrande = <i>Ctenocephalus</i>                      | <i>C. lyelli</i> Hicks = <i>Bailiella</i>   |
| <i>C. dalmani</i> Angelin = <i>Bailiaspis</i>                           | <i>C. malvernensis</i> Phillips = <i>Peltura</i>                                  |
| <i>C. cf. dalmani</i> Nicholas = <i>Bailiaspis</i><br><i>nicholasi</i>  | <i>C. matthewi</i> Hartt = <i>Ctenocephalus</i>                                   |
| <i>C. cf. dalmani</i> Sjörgren = <i>Bailiaspis</i><br><i>emarginata</i> | <i>C. mutica</i> Corda = <i>Conocoryphe</i>                                       |
| <i>C. elegans</i> Hartt = <i>Bailiaspis</i>                             | <i>C. perdita</i> Hicks = Undeterminable  |
| <i>C. emarginata</i> Linnarsson = <i>Bailiaspis</i>                     | <i>C. punctata</i> Corda = <i>Conocoryphe</i>                                     |
| <i>C. emarginata longifrons</i> Cobbold =<br><i>Bailiella</i>           | <i>C. pustulosa</i> Matthew = <i>Caintops</i>                                     |
| <i>C. exsulans</i> Linnarsson =<br><i>Ctenocephalus</i>                 | <i>C. quadrans</i> Miller = " <i>Ptychoparia</i> "                                |
| <i>C. frangtengensis</i> Reed = <i>Bailiella</i>                        | <i>C. reticulata</i> Walcott = <i>Atops</i>                                       |
| <i>C. gallatinensis</i> Meek = <i>Ehmania</i>                           | <i>C. rouayrouxi</i> Munier-Chalmas and<br>Bergeron = <i>Solenopleura ribeiro</i> |
| <i>C. geminispinosa</i> Miller =<br><i>Ctenocephalus</i>                | <i>C. tenuicincta</i> Linnarsson = <i>Bailiella</i>                               |
| <i>C. glabrata</i> Angelin = <i>Bailiaspis</i>                          | <i>C. teres</i> Grönwall = <i>Bailiella</i>                                       |
| <i>C. granulata</i> Corda = <i>Conocoryphe</i>                          | <i>C. trilineata</i> Ford = <i>Atops</i>  |
| <i>C. heberti</i> Munier-Chalmas and<br>Bergeron = <i>Bailiella</i>     | <i>C. ? variolaris</i> Salter = <i>Solenopleura</i>                               |
| <i>C. heberti pseudoculata</i> Miquel =<br><i>Bailiella</i>             | <i>C. (Erinnyis) venulosa</i> Grönwall =<br><i>Bailiella</i>                      |
|   | <i>C. viola</i> Woodward = Genus<br>indeterminate                                 |
|   | <i>C. walcotti</i> Matthew = <i>Bailiella</i>                                     |
|   | <i>C. williamsoni</i> Salter = <i>Beltella</i><br><i>bucephala</i>                |

It will be observed that besides the genotype *C. sulzeri*, several species remain in the genus. These include *C. ? humerosa* Salter from England and four species from Bohemia, *C. granulata*, *C. latifrons*, *C. mutica*, and *C. punctata*, differentiated by Corda from *C. sulzeri* with which they were subsequently placed by Barrande; they seem however, to be good species.

*C. lanenoisi* Mansuy from Tonkin, *C. frangtengensis* Reed from Kashmir, and *C. ulrichi* Resser and Endo from Manchukuo must be referred to *Bailiella*, if they do not constitute a new genus.

#### BAILIELLA Matthew, 1885

*Bailiella* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 103, 1885.

*Erinnys* SALTER, Quart. Journ. Geol. Soc. London, vol. 21, p. 746, 1865.

*Erinnys* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, pp. 84, 213, 1902.

*Salteria* WALCOTT, U. S. Geol. Surv. Bull. 10, p. 31, 1884.

Salter recognized the distinctness of these trilobites from *Conocoryphe*, but the name *Erinnys*, which he assigned to them, proved to be preoccupied; the same situation developed respecting Walcott's substitute *Salteria*. Matthew proposed *Bailiella* as a subgenus of *Conocoryphe* without recognizing the relationship between *B. baileyi* and *B. venulosa* Salter. Moreover, because Miller named *B. baileyi* as the genotype, the genus must rest on that species.

*Diagnosis*.—Cephalon semicircular; glabella well defined, tapered, with glabellar furrows. Eyes lacking. Fixed cheeks large, apparently extending to the lateral margins. Marginal furrow extends entirely around the cephalon. Rim generally of even width but sometimes slightly expanded in the middle. Preglabellar area always present and exceeds that of *Conocoryphe*.

Thorax and pygidium typical of the family.

Surface rarely smooth but usually pustulose or lined or both. Usually a ridge or vein extends outward across the cheeks from the dorsal furrow, arising near the front of the glabella. This ridge occupies the position of, and resembles, an eye line, but in some species it is more like a vein branching as it advances. Anterior to this ridge the system of surface ornamentation characterizing the species gives way frequently to lines or veins.

*Comparisons*.—Compared with *Conocoryphe*, *Bailiella* is readily distinguished by its wider preglabellar area and the absence of furrows across it. Its separation from *Bailiaspis* is less sharp because some species of *Bailiella* develop a slight thickening of the rim in the middle of the head.

*Genotype*.—*Conocephalites baileyi* Hartt.

*Range*.—Middle Cambrian of the Atlantic Province.



Besides the species presented below, the genus includes *Bailiella venulosa* Salter.

***Bailiella baileyi* (Hartt)<sup>2</sup>**

*Conocephalites baileyi* HARTT, in Dawson, *Acadian Geol.*, 2d ed., p. 645, 1868.

*Conocoryphe* (*Salteria*) *baileyi* WALCOTT, U. S. Geol. Surv. Bull. 10, p. 32, pl. 4, figs. 3, 3a, 1884.

*Conocoryphe* (*Bailiella*) *baileyi* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 111, pl. 1, figs. 22, 24, 25, 26, 27, 35, 1885.

Middle Cambrian, St. John (1c) ; Portland and other localities in New Brunswick.

***Bailiella arcuata* (Matthew)**

*Conocoryphe* (*Bailiella*) *baileyi arcuata* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 113, pl. 1, figs. 23, 23b, 1885.

Occurrence same as preceding.

***Bailiella walcotti* (Matthew)**

*Conocoryphe* (*Bailiella*) *walcotti* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 119, pl. 1, figs. 36, 36b, 1885.

Occurrence same as preceding.

***Bailiella aequalis* (Linnarsson)**

*Conocoryphe aequalis* LINNARSSON, *Sveriges Geol. Unders.*, ser. C, no. 54, p. 25, pl. 4, figs. 12-15, 1882.

Middle Cambrian, Tessini beds ; Andrarum, Sweden. Also identified from localities in Bornholm and England.

*Cotypes*.—*Sveriges G. U.* ; plesiotypes, Min. Mus. Copenhagen no. 159, Sedgwick Mus. no. A 47.

***Bailiella longifrons* (Cobbold)**

*Conocoryphe emarginata longifrons* COBBOLD, *Quart. Journ. Geol. Soc. London*, vol. 67, p. 286, pl. 24, figs. 8-13, 1911.

Middle Cambrian, Comley ; Shropshire, England.

*Cotypes*.—Sedgwick Mus. nos. A 61-A 65.

***Bailiella tenuicincta* (Linnarsson)**

*Conocoryphe tenuicincta* LINNARSSON, *Sveriges Geol. Unders.*, ser. c, no. 35, p. 18, pl. 2, figs. 23-25, 1879.

Middle Cambrian, Exsulans limestone ; Andrarum and other localities in Sweden, and Bornholm, Denmark.

*Holotype*.—*Sveriges G. U.*

<sup>2</sup>Hartt's types came to the museum at Cornell University and most of Matthew's to the Royal Ontario Museum at Toronto. Numbers are not now available for the types listed below.



**Bailiella bullata (Howell)**

*Conocoryphe bullata* HOWELL, Bull. Amer. Pal., vol. 2, no. 43, p. 87, pl. 3, figs. 10, 11, 1925.

Middle Cambrian, Manuels; Manuels Brook, Conception Bay, Newfoundland.

*Holotype*.—Princeton Univ. no. 8021; paratype, no. 8026.

**Bailiella lyelli (Hicks)**

*Conocoryphe lyelli* HICKS, Quart. Journ. Geol. Soc. London, vol. 27, p. 399, pl. 16, figs. 1-7, 1871.

*Conocoryphe (Liocephalus) lyelli* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, p. 84, 1902.

Middle Cambrian, Menevian; Nuns' Well, St. Davids, North Wales.

*Cotypes*.—Sedgwick Mus. nos. A 765, A 1090, A 1081; Mus. Pract. Geol. nos. 7613, 7614.

**Bailiella impressa (Linnarsson)**

*Conocoryphe impressa* LINNARSSON, Sveriges Geol. Unders., ser. C, no. 35, p. 20, pl. 2, figs. 29, 30, 1879.

*Conocoryphe (Liocephalus) impressa* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, p. 101, pl. 1, fig. 25, 1902.

Middle Cambrian, Exsulans limestone; Andrarum and other localities in Sweden and Bornholm.

*Holotype*.—Sveriges G. U.

**Bailiella cobboldi, n. sp.**

*Conocoryphe (Liocephalus) impressa* COBBOLD, Quart. Journ. Geol. Soc. London, vol. 69, p. 33, pl. 3, fig. 16, 1913.

This species differs from *B. impressa* in having a wider rim and a less tapered glabella.

Middle Cambrian, Comley; Shropshire, England.

*Holotype*.—Sedgwick Mus. no. A 50.

**Bailiella comleyensis, n. sp.**

*Conocoryphe aequalis* COBBOLD, Quart. Journ. Geol. Soc. London, vol. 69, p. 32, pl. 3, fig. 18, 1913.

The cephalic outline of this species is quite distinct from that of *B. aequalis*; the rim is also more thickened in the middle, the glabella narrower and the test smoother.

Occurrence same as preceding.

*Holotype*.—Sedgwick Mus. no. A 47.

**Bailiella teres (Grönwall)**

*Conocoryphe (Liocephalus) teres* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, pp. 103, 215, pl. 2, fig. 2, 1902.

Middle Cambrian, Exsulans; Borregaard, Bornholm, Denmark, and Skåne, Sweden.

*Holotype*.—Danmarks G. U.

**Bailiella heberti (Munier-Chalmas and Bergeron)**

*Conocoryphe heberti* MUNIER-CHALMAS and BERGERON, Ann. Sci. Geol., vol. 22, p. 334, pl. 3, figs. 3, 4, 1889.

Middle Cambrian; Montagne Noir, Hérault, France, and localities in Spain.

*Holotype*.—Presumably at the Univ. Paris.

**Bailiella pseudooculata (Miquel)**

*Conocoryphe heberti pseudooculata* MIQUEL, Bull. Geol. Soc. France, 4th ser., vol. 5, p. 474, pl. 15, fig. 6, 1905.

Middle Cambrian; Coulouma, Hérault, France.

*Holotype*.—Presumably at Montpellier.

**Bailiella levyi (Munier-Chalmas and Bergeron)**

*Conocoryphe levyi* MUNIER-CHALMAS and BERGERON, Ann. Sci. Geol., vol. 22, p. 335, pl. 3, fig. 1, 1889.

Occurrence same as *B. heberti*.

*Holotype*.—Presumably at the Univ. Paris.

**BAILIASPIS, n. gen.**

Several species that have been referred to *Conocoryphe* or *Ctenocephalus* differ in sufficient degree to warrant separate generic designation. These forms are nearest to *Bailiella*, being separated by the thickening, backward projection, and sometimes upturning of the rim in the middle of the cephalon, for which reason the name *Bailiaspis* is proposed.

*Diagnosis*.—All features normal for the family. Cephalon and pygidium like *Bailiella* except for the rim of cephalon. Rim thickened and extended backward in the middle, sufficiently in some species to connect the anterior furrow with the dorsal furrow.

Some species were referred to *Ctenocephalus* because the thickened rim simulates a median boss, but examination of the specimens shows at once that the structure is quite different.

*Genotype*.—*Conocephalites elegans* Hartt.

*Range*.—Same as for *Bailiella*.

**Bailiaspis elegans (Hartt)**

*Conocephalites elegans* HARTT, in Dawson, Acadian Geol., 2d ed., p. 650, 1868.  
*Conocoryphe elegans* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 115, pl. 1, figs. 28-33, 1885.

Middle Cambrian, St. John (1c); Ratcliffe Millstream, St. John, and other localities in New Brunswick.

*Holotype*.—R. O. M.

**Bailiaspis granulata (Matthew)**

*Conocoryphe elegans granulatus* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 116, pl. 1, fig. 34, 1885.

Occurrence same as preceding.

*Holotype*.—R. O. M.

**Bailiaspis dalmani (Angelin)**

*Conocoryphe dalmani* ANGELIN, Pal. Scand., 3d ed. Holmiae, p. 63, pl. 33, fig. 6, 1878.

Middle Cambrian, Exsulans limestones; Andrarum and other localities in Sweden and Bornholm.

*Holotype*.—Lund Univ.; plesiotypes, Sveriges G. U.

**Bailiaspis emarginata (Linnarsson)**

*Conocoryphe emarginata* LINNARSSON, Geol. Foren, Stockholm Förhandl., vol. 3, p. 366, pl. 15, figs. 2-4, 1877.

Middle Cambrian, Ölandicus zone; Stora Frö, Öland, Sweden.

*Cotypes*.—Sveriges G. U.

**Bailiaspis bufo (Hicks)**

*Conocoryphe bufo* HICKS, British Assoc. Rep., p. 285, 1865.

*Conocoryphe bufo* HICKS, Quart. Journ. Geol. Soc. London, vol. 25, p. 52, pl. 2, fig. 8, 1869.

*Conocoryphe bufo* ILLING, idem, vol. 71, p. 425, pl. 35, figs. 1-3, 1915.

*Bailiella bufo* REED, Geol. Mag., dec. 4, vol. 5, p. 493, 1898.

Middle Cambrian, Menevian; Porth-y-rhaw, St. Davids, North Wales.

*Holotype*.—Mus. Pract. Geol.; plesiotypes, Sedgwick Mus. nos. A 48, A 224.

**Bailiaspis glabrata (Angelin)**

*Conocoryphe ? glabrata* ANGELIN, Pal. Scand., 3d ed. Holmiae, p. 72, pl. 37, fig. 8, 1878.

Middle Cambrian, Andrarum; Andrarum and other localities in Sweden and Bornholm.

*Holotype*.—Riksmus. Stockholm.

**CTENOCEPHALUS Corda, 1847**

*Ctenocephalus* CORDA, Abh. k. bömischen Gessell. Wiss., vol. 5, p. 142, 1847.

*Ctenocephalus* MATTHEW, Trans. Roy. Soc. Canada, vol. 4, p. 103, 1885.

*Ctenocephalus* GRÖNWALL, Danmarks Geol. Unders., vol. 2, p. 84, 1902.

*Elyx* ANGELIN, Pal. Scand., 3d ed., Holmiae, p. 4 (1854), 1878. (Misprinted *Eryx*.)

*Hartella* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 103, 1885.

It is possible that *Elyx* might be established as a distinct genus because of the angular outline, but since otherwise it agrees with *Ctenocephalus*, present usage is continued.

Matthew erected *Hartella* as a subgenus of *Ctenocephalus*, stating that both had a frontal lobe anterior to the glabella but that *Ctenocephalus* had a "wall-like front to the cheeks and frontal lobe," whereas *Hartella* had "a sloping front to the cheeks and frontal lobe." He further characterized both genera as having a small pygidium in contradistinction to *Conocoryphe*. The mentioned difference in the anterior portions of the head might be interpreted as indicating separate genera, but because there seems to be an intergradation in this respect from species to species, it seems wiser to drop *Hartella*.

*Genotype*.—*Conocephalus coronatus* Barrande.

*Range*.—Same as *Conocoryphe*.

Species previously referred to *Ctenocephalus*:

*C. coronatus* (Barrande)

*C. latilimbatus* (Brögger) [doubtful]

*C. exsulans* (Linnarsson)

*C. tumidus* Grönwall

*C. laticeps* (Angelin)

In addition there are the species previously referred to the subgenus *Hartella*:

*C. matthewi* (Hartt)

*C. perhispidus* (Matthew)

*C. hispidus* (Matthew)

Besides these eight species, several that were suppressed appear to deserve full recognition. They are listed below.

***Ctenocephalus geminispinosus* (Hartt)**

*Conocephalites gemini-spinosus* HARTT, in Dawson, Acadian Geol., 2d ed., p. 653, 1868.

*Ctenocephalus* (*Hartella*) *matthewi geminispinosus* MATTHEW, Trans. Roy. Soc. Canada, vol. 2, sec. 4, p. 106, 1885.

Middle Cambrian, St. John (1c) ; localities in New Brunswick.

*Holotype*.—Cornell Univ.

***Ctenocephalus hartti*, n. sp.**

*Conocoryphe* (Subgenus?) *matthewi* WALCOTT (part), U. S. Geol. Surv. Bull. 10, p. 28, pl. 4, fig. 1, 1884 (not 1a = *C. hispida*).

This species is distinguished by the system of veins underlying the scattered granules. Moreover, the veins increase in strength on the anterior portions of the cheeks beyond the raised lines which extend

out from the anterior portion of the glabella or rather the dorsal furrow.

Occurrence same as preceding.

*Holotype*.—Presumably R. O. M.

**Ctenocephalus granulatus (Walcott)**

*Conocoryphe* (Subgenus?) *matthewi granulata* WALCOTT, U. S. Geol. Surv.

Bull. 10, p. 30, pl. 4, fig. 1b, 1884.

*Conocoryphe elegans* WALCOTT (part), idem, pl. 4, fig. 2a.

Occurrence same as preceding.

*Holotype*. Cornell Univ.

**HOLOCEPHALINA Salter, 1864**

*Holocephalina* SALTER, Quart. Journ. Geol. Soc. London, vol. 20, p. 237, 1864.

*Holocephalina* ILLING, idem, vol. 71, p. 424, 1915.

*Liocephalus* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, pp. 84, 213, 1902.

Grönwall designated *Conocoryphe impressa* Linnarsson as the genotype of his subgenus *Liocephalus*. This species, together with *C. lyelli*, belongs to *Bailiella*, which fact alone would invalidate *Liocephalus*. However, it seems that Grönwall's concept of *Liocephalus* was that of Salter's *Holocephalina*, which, being the earlier name, must be the recognized genus. Moreover, Grönwall described a good species of *Holocephalina* as *L. linnarssoni*.

*Diagnosis*.—A rather small trilobite with convex cephalon. Glabella distinctly marked by shallow dorsal furrow. Marginal furrow also shallow; thorax and pygidium typical of the family.

*Comparisons*.—*Holocephalina* needs only to be compared with *Hartshillia* and the new genus *Dasometopus*. Illing has already distinguished the first two, and the features of the last named are presented with its discussion.

*Genotype*.—*H. primordialis* Salter.

*Range*.—Same as *Conocoryphe*.

Three species have been recognized previously in the genus, *H. primordialis*, *H. holocephala* Miquel, and *H. incerta* Illing.

**Holocephalina linnarssoni (Grönwall)**

*Conocoryphe* (*Liocephalus*) *linnarssoni* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, pp. 102, 214, pl. 2, fig. 1, 1902.

Middle Cambrian, Exsulans limestone; Borregaard, Bornholm, Denmark.

*Holotype*.—Min. Mus. Copenhagen.

**DASOMETOPUS, n. gen.**

This peculiar trilobite was originally referred by Angelin to *Harpides*. Subsequently, Grönwall placed it in the invalid genus *Erinnys*, thus including the species in *Bailiella*. Only a brief examination is necessary to show that this form is not *Bailiella*; consequently, a new genus must be made for it.

*Diagnosis*.—Cephalon alone known. Cephalon semicircular, eyeless. Glabella well defined, tapered, a little more than half the length of the head. Glabellar furrows present, the rear pair recurved, separating marginal lobes. Cheeks marked by irregular lines radiating from the dorsal furrow. Upturned rim with coarse granules; other scattered granules on cheeks. A depression extends across the preglabellar area.

*Comparisons*.—*Dasometopus* is similar to *Holocephalina* in many respects. It differs in its greater relative width and particularly in the depression extending from the glabella to the anterior furrow. From *Bailiella* it is also differentiated by this depression.

*Genotype*.—*Harpides breviceps* Angelin.

*Range*.—Middle Cambrian of the Atlantic Province.

*Name*.—*δασνς* = rough, *μετωπον* = forehead.

***Dasometopus breviceps* (Angelin)**

*Harpides breviceps* ANGELIN, Pal. Scand., 3d ed., Holmiae, p. 87, pl. 41, fig. 8, 1878 (1st ed., 1854).

*Conocoryphe (Erinnys) breviceps* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, p. 97, 1902.

Middle Cambrian, Andrarum; Andrarum, Sweden and Bornholm, Denmark.

**CORYNEXOCHIDAE Angelin, 1852****CORYNEXOCHUS Angelin, 1852**

*Corynexochus* ANGELIN, Pal. Scand., 3d ed., Holmiae, p. 59, 1878 (earlier editions 1852, 1854).

*Corynexochus* GRÖNWALL, Danmarks Geol. Unders., vol. 2, no. 13, p. 136, 1902.

*Corynexochus* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 309, 1916.

*Corynexochus* RAYMOND, Amer. Journ. Sci., vol. 15, p. 309, 1928.

*Corynexochus* LAKE, Mon. British Camb. Tril., Pal. Soc., pt. 8, p. 180, 1934.

*Karlia* WALCOTT, Proc. U. S. Nat. Mus., vol. 11, p. 444, 1880.

Angelin founded *Corynexochus* on a cranium, but as pointed out by Lake, the specific name of the genotype evidently was based on a spinose tail. Some doubt still remains regarding the pygidium, but Grönwall's assignment of a small pygidium to Angelin's species appears to be correct.



Walcott evidently intended to base his genus *Karlia* on the Mount Stephen species, *K. stephenensis*, but according to the rules of nomenclature, because Miller designated Walcott's first species *K. minor* as the genotype, *Karlia* must rest on that species. However, *K. minor* is a real *Corynexochus*; hence *Karlia* becomes a synonym, and the new generic name, *Bonnaspis*, is given to *K. stephensis* because it evidently is related to *Bonnia* and is not to be regarded as belonging to the family Corynexochidae.

Raymond and Walcott confused trilobites of several families with *Corynexochus*. Subsequently, Lake reviewed the group and pointed out the need for rearrangement. In confining the genus to its proper limits, a new diagnosis becomes necessary.

*Diagnosis*.—Small trilobites with large glabella extending to the anterior edge. Glabella expanded forward so that its width at the front end is about twice that dimension at the neck ring; short, faint glabellar furrows present. Eyes small, situated forward of the midpoint. Fixed cheeks wide in rear, tapering rapidly to extinction at the anterior end of the eyes, except for tiny anterior lobes.

Thorax in *C. minor* has seven segments.

Pygidium small, flat, with segments fused. Axial and pleural furrows present.

*Genotype*.—*C. spinulosus* Angelin.

*Range*.—Middle Cambrian of the Atlantic Province.

Besides the genotype *C. spinulosus*, *Corynexochus* then includes the previously assigned species *C. bornholmiensis* Grönwall from Bornholm; *C. cambrensis* Nicholas and *C. pusillus* Illing from England; *C. delagei* Miquel from southern France; and *C. minor* (Walcott) from Newfoundland.

*C. stephensis* becomes the type of the new genus *Bonnaspis*, and the Lower Cambrian species are to be referred to *Bonnia*.

#### HOUSIA Walcott, 1924

##### *Housia vacuna* (Walcott)

*Ptychoparia vacuna* WALCOTT, Proc. U. S. Nat. Mus., vol. 13, p. 275, pl. 21, figs. 8, 12, 1890.

Upper Cambrian, Deadwood; (loc. 88a) Spring Creek Canyon, Black Hills, South Dakota.

*Holotype*.—U.S.N.M. no. 23862.



**INGLEFIELDIA Poulsen, 1927**

*Inglefieldia* POULSEN, Meddels. Grønland, vol. 70, p. 261, 1927.

*Inglefieldia* RESSER, Smithsonian Misc. Coll., vol. 93, no. 5, p. 36, 1935.

Further study of the Appalachian and other Lower Cambrian trilobites shows the necessity of referring additional species to *Inglefieldia*, even after certain groups are separated as new genera. Arbitrary limits must be set to separate *Inglefieldia* from *Kochiella* on the one hand and from *Poulsenia* and *Antagmus* on the other. If the brim increases in width and is flattened, the species passes into *Kochiella*. If, however, the rim thickens and the cranidium becomes more convex in all its parts, the species is referable to *Poulsenia*. Finally, if the thickening of the rim is accompanied by a reduction in width of the preglabellar area with a concomitant increase in the backward projection of the rim in the middle, the species becomes *Antagmus*.

Hitherto *Inglefieldia* contained the following species:

*I. porosa* Poulsen

*I. discreta* Poulsen

*I. planilimbata* Poulsen

*I. thia* Poulsen

*I. groenlandica* Poulsen

*I. venulosa* (Poulsen)

*I. inconspicua* Poulsen

***Inglefieldia affinis* Poulsen**

*Inglefieldia affinis* POULSEN, Meddels. Grønland, vol. 70, p. 264, pl. 15, fig. 23, 1927.

This species is on the border of the genus but for the present may be retained in it.

Lower Cambrian, Cape Kent; Cape Kent, northwest Greenland.

**KINGSTONIA Walcott, 1924**

*Kingstonia* WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 58, 1924; idem, no. 3, p. 103, 1925.

*Ucebia* WALCOTT, idem, pp. 60, 118.

It is possible that *Stenopilus* Raymond is also synonymous, but further study is necessary to prove this point.

*Genotype*.—*K. apion* Walcott.

*Range*.—Apparently in the earlier beds of the Upper Cambrian.

***Kingstonia ara* (Walcott)**

*Ucebia ara* WALCOTT, Smithsonian Misc. Coll., vol. 75, no. 2, p. 60, pl. 14, fig. 4, 1924; idem, no. 3, p. 118, pl. 17, figs. 7, 8, 1925.

Upper Cambrian, Warrior; (loc. 107k) 1 mile southeast of Warriors Mark, Pennsylvania.

*Cotypes*.—U.S.N.M. nos. 70257, 70258.

***Kingstonia globosa* (Walcott)**

*Agraulos? globosus* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 61, pl. 9, fig. 23, 1884.

In this and related species the glabella is more convex than the remainder of the cranidium and hence appears more distinctly separated than in the genotype.

Upper Cambrian, Secret Canyon; (loc. 59) Combs Peak, and (loc. 61) Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24559.

#### LABRADORIA, n. gen.

A single species among the abundant Lower Cambrian trilobites of the Forteau formation can be referred to no other genus and must, therefore, be given a name. It is likely, however, that additional species will be discovered among the large collections from beds of similar age in the Appalachians.

*Diagnosis*.—Cranidium alone known. Glabella large, convex, rising above the fixed cheeks and extending forward to the rim. A strong occipital furrow separates a neck ring which is extended into a stout spine. Three sets of glabellar furrows extend across the glabella, sloping backward in the usual manner. Eyes fairly large, situated well back. Eye lines heavy. Brim consists of a thickened rim only. Facial sutures diverge slightly anterior to the eyes.

*Genotype*.—*Conocephalites miser* Billings.

*Range*.—Lower Cambrian of the Appalachians.

#### *Labradoria miser* (Billings)

*Conocephalites miser* BILLINGS, Geol. Vermont, vol. 2, p. 950, fig. 354, 1861;

Pal. Foss., Geol. Surv. Canada, pt. 1, p. 11, fig. 14, 1861.

*Ptychoparia miser* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 199, pl. 27, fig. 2, 1886; 10th Ann. Rep. U. S. Geol. Surv., p. 651, pl. 96, fig. 8, 1891.

Billings described the species, illustrating only the glabella. Subsequently, Whiteaves and Walcott restudied Billings' material, and Walcott published a figure of a more complete specimen, which thus became the neoholotype and on which the species must rest.

Lower Cambrian, Forteau; L'Anse au Loup, Straits of Belle Isle, Labrador.

*Neoholotype*.—Nat. Mus. Canada; cast, U.S.N.M. no. 15444.

#### MODOCIA Walcott, 1924

#### *Modocia penfieldi* (Walcott)

*Ptychoparia penfieldi* WALCOTT, U. S. Geol. Surv. Mon. 32, pt. 2, p. 456, pl. 65, figs. 4-4b, 1899.

Upper Cambrian; south side Gallatin Valley, northwestern Yellowstone Park, Wyoming.

*Cotypes*.—U.S.N.M. no. 35231.

## PLETHOPELTIS Raymond, 1913

*Plethopeltis levis* (Walcott)

*Arionellus levis* WALCOTT, U. S. Geol. Surv. Mon. 32, p. 462, pl. 65, fig. 1, 1899.

Upper Cambrian; Crowfoot Ridge, northwestern Yellowstone National Park, Wyoming.

*Holotype*.—U.S.N.M. no. 35230.

## POULSENIA, n. gen.

Associated with *Inglefieldia* in Greenland and elsewhere in the Appalachians are many species of a closely related trilobite. Poulsen set these species off by assigning them to *Solenopleura*, whereas Walcott placed the more southerly forms in *Ptychoparia*.

*Diagnosis*.—Small trilobites of average form. Cranidium rather wide, convex in both directions; facial sutures diverging slightly anterior to the eyes, but owing to the infolding of the anterior angles appear to converge. Glabella well defined, tapering, truncated or rounded in front; two thirds or more of the length of the cranidium. Glabellar furrows two or three short pairs; neck furrow and ring well defined. Eyes small, situated in middle or somewhat back of the middle of the head. Eye lines present, brim consisting of a more or less thickened rim and a preglabellar area of varying relative width.

Judging from somewhat uncertain material, the thorax consists of about 15 segments. Pygidium small, well fused, with axis well defined, and with pleural grooves.

*Genotype*.—*Solenopleura grönwalli* Poulsen.

*Range*.—Upper Lower Cambrian of North America.

*Comparisons*.—Superficially *Poulsenia* resembles the Atlantic Province Middle Cambrian genus *Solenopleura*, but it is doubtful if this resemblance involves any relationship. On the other hand, *Poulsenia* appears simply to be the convex forms of the *Inglefieldia* stock.

*Poulsenia grönwalli* (Poulsen)

*Solenopleura grönwalli* POULSEN, Meddels. Grønland, vol. 70, p. 265, pl. 15, fig. 28, 1927.

Lower Cambrian, Cape Kent; Cape Kent, northwest Greenland.

*Holotype*.—Min. Mus. Copenhagen; cast, U.S.N.M. no. 70980.

*Poulsenia similis* (Poulsen)

*Solenopleura similis* POULSEN, Meddels. Grønland, vol. 70, p. 265, pl. 15, fig. 26, 1927.

Occurrence same as preceding.

*Holotype*.—Min. Mus. Copenhagen; cast, U.S.N.M. no. 70981.

**Poulsenia bullata (Poulsen)**

*Solenopleura bullata* POULSEN, Meddels. Grønland, vol. 70, p. 266, pl. 15, figs. 24, 25, 1927.

Occurrence same as preceding.

*Holotype*.—Min. Mus. Copenhagen; cast, U.S.N.M. no. 70948.

**Poulsenia borealis (Poulsen)**

*Solenopleura borealis* POULSEN, Meddels. Grønland, vol. 70, p. 266, pl. 15, fig. 27, 1927.

Occurrence same as preceding.

*Holotype*.—Min. Mus. Copenhagen.

**PTARMINGIA Raymond, 1928****Ptarmingia gordonensis, n. sp.**

*Albertella helena* WALCOTT (part), Smithsonian Misc. Coll., vol. 53, no. 2, p. 19, pl. 2, fig. 5, 1908 (see *Albertella helena*).

The Montana species has about the same proportions as *P. rossensis*, but the eyes are smaller and the brim reduced.

Middle Cambrian, Gordon; (loc. 4v) Gordon Creek, Lewis and Clark Range, Montana.

*Holotype*.—U.S.N.M. no. 53408.

**STENOCHILINA Ulrich, 1930****Stenochilina matutina (Hall)**

*Amphion? matutina* HALL, 16th Ann. Rep. N. Y. State Cab. Nat. Hist., p. 222, pl. 5a, fig. 6, 1863; Trans. Albany Inst., vol. 5, p. 194, 1867.

*Amphion? matutina* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 219, pl. 26, fig. 8, 1916.

The original description reads as follows:

Glabella gibbous, longer than wide, subovate, rounded and a little wider in front. Occipital ring narrow and straight; occipital furrow narrow. Posterior lobe a little oblique, the furrow deeply impressed and a little expanded at its inner extremity; median lobe with the sides nearly parallel, separated from the anterior lobe by a narrow distinct furrow; anterior lobe broad, the length somewhat less than half the entire length of the glabella, a scarcely defined depression extending obliquely from near the middle of its length to the front.

It seems that this species, which has been unplaced generically for many years, can be definitely put into *Stenochilina*.

Upper Cambrian, Eau Claire; (loc. 84) Trempealeau, Wisconsin. Also reported from Dresbach, Minnesota.

*Holotype*.—A.M.N.H. no. 349; plesiotype, U.S.N.M. no 61592.

**SYSPACEPHALUS, n. gen.**

*Diagnosis*.—Small trilobites of which the cranidium alone is known. Glabella narrow, tapering slightly; truncated, about two-thirds as long as cranidium; in some species ill defined on upper surface of test. Glabellar furrows showing on inner side of test. Brim convex with faint frontal furrows extending inward from the anterior angles for varying distances. Facial suture converging anterior to eyes. Eyes small. Occipital furrow developed on the cheeks, but sometimes almost obsolete on the cranidium.

*Genotype*.—*Agraulos charops* Walcott.

*Range*.—Late Lower Cambrian. Upper Mount Whyte and formations of a similar age.

*Name*.—συσπαω = contracted; κεφαλος = head.

**Syspacephalus charops (Walcott)**

*Agraulops charops* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 72, pl. 13, fig. 2, 1917.

Lower Cambrian, Mount Whyte; (loc. 35f) Mount Stephen, near Field, British Columbia.

*Holotype*.—U.S.N.M. no. 64395.

**Syspacephalus unca (Walcott)**

*Agraulos? unca* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 73, pl. 13, fig. 1, 1917.

Lower Cambrian, Mount Whyte; (loc. 61d) Mount Shaffer and (loc. 35h) Mount Bosworth, British Columbia.

*Holotype*.—U.S.N.M. no. 64394.

**Syspacephalus? redpathi (Walcott)**

*Agraulos redpathi* WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 654, fig. 69, 1891.

Lower Cambrian; Mount Simon, Quebec.

*Cotypes*.—U.S.N.M. no. 23839; Peter Redpath Mus., McGill University, Montreal.

**OLIGOMETOPUS, n. gen.**

*Diagnosis*.—Cranidium only part known. Broad, with wide glabella and fixed cheeks. Glabella wide, rounded in front, apparently with a faint rear pair of joined glabellar furrows. Eyes slightly behind middle of head; eye lines developed. Brim consists of narrow rim only.

*Genotype*.—*Ptychoparia* (*Solenopleura*?) *breviceps* Walcott.

*Range*.—Upper Cambrian.

*Name*.—ολιγος = little ; μετοπον = forehead.

**Oligometopus breviceps (Walcott)**

*Ptychoparia* (*Solenopleura*?) *breviceps* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 49, pl. 10, fig. 9, 1884.

*Pagodia breviceps* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, pl. 361, no. 13, 1914.

Upper Cambrian, Secret Canyon (loc. 62) ; near Adams Hill, Eureka district, Nevada.

*Holotype*.—U.S.N.M. no. 24577.





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WITH THEM

(WITH EIGHT PLATES)

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# MOLLUSCAN INTERMEDIATE HOSTS OF THE ASIATIC BLOOD FLUKE, SCHISTOSOMA JAPONICUM, AND SPECIES CONFUSED WITH THEM

By PAUL BARTSCH

*Curator of Mollusks and Cenozoic Invertebrates, U. S. National Museum*

(WITH EIGHT PLATES)

## INTRODUCTION

The importance which certain groups of insignificant-looking, small mollusks possess, because they have been proved to serve as intermediate hosts in part of the life history of parasites that in their adult stage affect man or his domestic animals, is demonstrated by the number of pages that have been devoted to them in the medical, scientific, and popular press.

Prior to the discovery of the Japanese blood fluke of man, *Schistosoma japonicum* Katsurada, by Miyairi and Suzuki in 1913, and the working out of its life history in Japan, little attention was paid to the mollusks serving as intermediate hosts for that dire disease-producing organism. In fact, the species involved in the Japanese Empire were unknown to science at the time.

The brilliant researches by Japanese investigators were the first to make known definitely that an intermediate host problem existed in schistosomiasis. These and other studies demonstrated that an inconspicuous amphibious mollusk shared with man, the dog, cat, cattle, and rat, an ailment that may affect, as recorded by Faust (48, p. 432), a hundred million inhabitants of China, as well as many in Japan and a lesser number in Formosa and the Philippines.

The molluscan material from the Asiatic continent and off-lying islands, particularly the inconspicuous fresh-water animals, had up to this time received scant attention. They had little to commend them to humanity at large, and the number of molluscan students collecting them were few and their endeavors restricted to limited localities. It is therefore not surprising that our knowledge of them was as fragmentary as it proved to be at the time that schistosomiasis in Japan came to the fore. Even now, as this paper will show, the subject is not exhausted, but enough information is at hand to point a way for future exploration in the molluscan field and to show its medical importance.

I believe most of the medical men who have to deal with Asiatic schistosomiasis and particularly the control problem connected therewith have chafed, to say the least, under the inconsistency of names used in the writings of the intermediate host students. But they should consider this to be in the nature of growing pains.

The mixed concepts which the molluscan pages reveal are undoubtedly due to the lack of adequate material for comparative study, the authors adding small fragments from time to time as these became available. It seems to me that now we have sufficient adequately preserved material in the collections of the United States National Museum of almost all the forms to attempt an exhaustive comparative study.

I have given a separate historical account and discussion under each genus here considered, feeling that this will prove most helpful to the workers occupying the definite areas inhabited by these animals. This will enable them to recognize more readily the species involved in the intermediate host problem of Asiatic schistosomiasis and to exonerate some innocents.

There are many people to whom acknowledgment should be made for helpfulness in making this endeavor as complete as it is. First I should mention those who have contributed material. Among these are, outstandingly, Dr. H. A. Pilsbry, of the Philadelphia Academy of Natural Sciences, Dr. Fu-ching Li, of Honan University, Kaifeng, Honan, China, Dr. Y. T. Yao, Director of the Central Field Health Station, National Government of the Republic of China, Dr. E. A. Faust, of Tulane University, New Orleans, La., Dr. H. E. Meleney, Vanderbilt University, Nashville, Tenn., Dr. Sado Yoshida, Pathological Institute, Osaka Imperial University, Osaka, Japan, Dr. Mary N. Andrews, of the Henry Lester Institute of Medical Research, Shanghai, China, and many others, particularly the early molluscan collectors whose efforts are recorded with material in the collection of the United States National Museum, outstanding among whom are von Möllendorff, Quadras, and A. Adams.

I am also indebted to the members of my staff, Dr. J. P. E. Morrison, who has made the radula and opercula preparations and supervised the careful drawing thereof by our artist, Mrs. Aime M. Awl, and to Dr. Harald A. Rehder for much helpfulness.

The four genera here discussed are *Blanfordia*, *Katayama*, *Oncomelania*, and *Schistosomophora*.

The species of *Blanfordia*, as far as known, are innocent of taking a part in schistosomiasis. The name, however, has been erroneously applied to the true menace in Japan, Formosa, and parts of China.

It is deemed wise here to give reasons why a clean bill of health is bestowed upon them.

The most important genus, as far as Asiatic schistosomiasis is concerned, is *Katayama*, which ranges from southern Japan through Formosa, to Canton, China.

In China by far the most important intermediate hosts are the various species of *Oncomelania*, all of which, whether technically demonstrated as intermediate hosts or not, should be looked upon as a potential menace.

The last genus, *Schistosomophora*, established in this paper, includes the newly demonstrated host of *Schistosoma* in the southern Philippines; one species not yet a demonstrated host is found in the Island of Honshu, Japan.

I will now give a series of keys which I believe will prove helpful to students in the identification of these genera.

KEY TO THE RADULAE OF THE GENERA OF THE INTERMEDIATE HOSTS  
OF SCHISTOSOMA JAPONICUM

- Rachidian tooth 3-cusped in adults <sup>1</sup>
  - Basal denticles 3-3.....*Katayama*.
  - Basal denticles 2-2.....*Oncomelania*.
- Rachidian tooth 5-cusped in adults <sup>1</sup>
  - Basal denticles 2-2.....*Schistosomophora*.
  - Basal denticles 4-4.....*Blanfordia*.<sup>2</sup>

KEY TO THE OPERCULA OF THE GENERA OF THE INTERMEDIATE  
HOSTS OF SCHISTOSOMA JAPONICUM

- Whorls 1.5 .....*Schistosomophora*.
- Whorls 2.2
  - Nucleus very excentric.....*Oncomelania*.
  - Nucleus not very excentric.....*Blanfordia*.
- Whorls 3.2 .....*Katayama*.

Unfortunately, the characters of the shells are not as clear cut as the radula and opercula, and their placement in a key would be rather involved. Suffice it to say here that *Oncomelania*, always, as far as we know, has the shell axially ribbed; *Katayama* in Japan and China has the shell elongate-conic, but in the Formosan species it is ovate, thus resembling *Blanfordia* and *Schistosomophora*. The *Blanfordias* are larger than the *Schistosomophoras*, excepting *Blanfordia integra*, which is almost as small.

<sup>1</sup> In very young mollusks or unworn parts of the radula a slight outer third cusp may be present on each side of the central tooth.  
<sup>2</sup> No species of the genus *Blanfordia* as here limited has so far been implicated as intermediate host of *Schistosoma japonicum*.



## DESCRIPTION OF GENERA AND SPECIES

## BLANFORDIA

*Genotype*.—*Tomichia bensoni* A. Adams.

The name *Blanfordia* has so frequently been associated with mollusks serving as intermediate hosts for the Asiatic blood fluke that I have felt it necessary here to go into convincing details to show that there is no excuse for this. The species belonging to this genus form a compact small group whose distribution is limited to northern Japan, north of the schistosomophorous Katayamas.

## HISTORY

In 1861 Arthur Adams (1, p. 308)<sup>3</sup>, a ship surgeon in the British Navy and an indefatigable student of mollusks, which he appears to have gathered in every port made by ships on which he traveled, described among other things two new species from Japan, namely, *Tomichia bensoni* from Hokkaido and *Tomichia japonica* from Sado. Finding that these two species were not congeneric with *Tomichia*, he created for them in 1863 (2, p. 424) the new genus *Blanfordia*. *Tomichia japonica* Adams thus became *Blanfordia japonica* Adams and *Tomichia bensoni* Adams, *Blanfordia bensoni* Adams. Here he states:

In Japan, at Matsumai and Sado, I discovered two species of terrestrial Mollusks, with similar animals, which (in the "Annals" for October 1861) I referred to the genus *Tomichia*, Benson, a form of Truncatellidae from the Cape [Good Hope]. Since then, I have sent specimens of the shells, accompanied by drawings of the animals, to Mr. Benson; and he assures me that his *Tomichiae* are very different. He writes to me as follows:

"A comparison of the animal of the Cape *Tomichia* with that of your Japanese shells leads to the impression that your discoveries belong to a distinct genus, which, but for the operculum, may rather be regarded as a land-shell. I have examined a specimen, and find it horny and subspiral in construction, the same as that of *Tomichia*, but more solid."

After describing the genus, Adams states that the tentacles are short and triangular, that the eyes are sessile on the upper base of the tentacles, that the foot is lobed on each side in front with a posterior dorsal lobe which bears the operculum. He further states that both of his species were found on damp banks covered with vegetation in rocky situations near the sea. He dedicated the genus to his friend, W. T. Blanford, a student of Indian mollusks, and

<sup>3</sup> Numbers in parentheses refer to list of references cited at end of paper.

figures the animal of *Blanfordia japonica* on plate 7 as figure 12, and *Blanfordia bensoni* on plate 7, figure 11.

In 1876 Pfeiffer (3, p. 22) lists *Blanfordia japonica* and *Blanfordia bensoni* and also other species which do not belong in this genus.

In 1878 Nevill (4, p. 254) fixed the type of *Blanfordia* by designating *Blanfordia bensoni* as type species.

A long interval passed before reference is again made to this genus. In 1897 von Möllendorff (11, p. 32) redescribed *Blanfordia bensoni* A. Adams from material collected by B. Schmacker near the city of Hakodate, Jeso, Japan.

In 1900 Dr. Pilsbry (13, p. 12) renamed *Blanfordia bensoni*, calling it *Pomatiopsis hirasei*, which becomes a synonym of *Blanfordia bensoni*.

In the same year (1900) von Möllendorff (12), after referring to his former treatise on *Blanfordia bensoni*, described *Blanfordia japonica*, which he states was collected by Hirase on Sado, *i. e.*, the type locality.

Pilsbry (14), in 1901, in his "Notes on the Recent Literature of Japanese Land-Snails", places his *Pomatiopsis hirasei* in the synonymy of *Blanfordia bensoni* Adams, and bestows the name *Blanfordia bensoni* var. *minor* upon the mollusk described under the name *Blanfordia japonica* by von Möllendorff. With this dictum I do not agree, but hold that von Möllendorff was correct.

The following year Pilsbry (15, pp. 26-27) again discussed *Blanfordia japonica* and *Blanfordia bensoni* and described *Blanfordia japonica* var. *simplex* as new from Nishigo, Uzen (Honshu Id.).

In 1903 Pilsbry (16, p. 114) again refers to *Blanfordia japonica* from Sado Island, and raises his subspecies *Blanfordia japonica* var. *simplex* to specific rank.

For 12 years no papers appear in the malacological press, but in 1915 Dr. Pilsbry (23) again reviews "The Japanese Species of *Blanfordia*" and wrongly places *Katayama nosophora* in this genus. He again lists *Blanfordia japonica*, *Blanfordia bensoni*, and *Blanfordia simplex* and with them *Blanfordia nosophora* and figures all four and gives a key to them.

Here, too, he wrongly designates *Blanfordia japonica* as type of the genus *Blanfordia*, this having been established by Nevill in 1878 to be *Blanfordia bensoni* A. Adams.

Nine years later, 1924, Pilsbry (30) adds another species, *Blanfordia integra*, from Makuragisan, Izumo (Honshu Id.) to this genus. Here also he establishes the subgenus *Vicina*, with *Pomatiopsis hirasei* as type, which he says is apparently synonymous with

*Blanfordia bensoni*. He states that the subgenus also includes *Blanfordia simplex* Pilsbry. This subgenus, *Vicina*, therefore was still-born, as it is a pure and simple synonym of *Blanfordia*, having the same type.

The same year Annandale (31) published his paper on "The Molluscan Hosts of the Human Blood Fluke in China and Japan, and Species Liable to be Confused with Them." Here he gives a description of the animal, which I copy under the generic definition. He rightfully considers *Blanfordia* generically distinct from the rest of the complex. He gives a new name to *Blanfordia japonica*, namely, *Blanfordia pilsbryana*, from the type locality of *Blanfordia japonica*, naming it from Pilsbry's figures 1 and 2, Nautilus, 1915, page 2. He also wrongly lumps *Blanfordia simplex* under *Blanfordia bensoni*.

In 1928 Bequaert (37) published two papers on "Mollusks of Importance in Human and Veterinary Medicine." In this he places the Japanese intermediate hosts in *Blanfordia* and the Chinese in *Hemibia*.

Thiele (38) in 1929 recognized *Blanfordia* A. Adams as distinct from *Oncomelania* Gredler. He cites also the subgenus *Vicina*.

In 1932 Tubangui (40) published a paper on "The Molluscan Intermediate Host in the Philippines of the Oriental Blood Fluke, *Schistosoma japonicum* Katsurada." Here he cites *Blanfordia quadrasi* (= *Prososthenia quadrasi* Möllendorff) as host. He says this is most closely related to *Blanfordia formosana* Pilsbry and Hirase. He also says that the mollusks can stand prolonged desiccation, at least up to 4 weeks, under laboratory conditions. This is the *Schistosomophora hydrobiopsis* Rensch described in this paper.

Two years after this, in 1934, Bequaert (44) discusses the intermediate host of the Asiatic blood fluke in the Philippines and reviews the field as a whole on the basis of what has been said before. He places all the species in *Blanfordia*, which, as we have shown in the present effort, is not tenable.

The Philippine mollusk implicated is Rensch's *Oncomelania hydrobiopsis*, here made congeneric with *Prososthenia quadrasi* Möllendorff, which I am now rechristening *Schistosomophora quadrasi*; he calls it *Blanfordia quadrasi*.

Following Bequaert's paper in the same journal is a review of the subject by Pilsbry (45) which is largely devoted to a criticism of Annandale's effort, and supports Bequaert's contention.

#### GENERIC DEFINITION

*Shell*.—Shell ovate, thin, with inflated whorls which are marked by irregular incremental lines that in some species almost attain the

strength of threads, and spiral lirations which vary in different species from mere indications to well pronounced. The nuclear whorls (tip), usually eroded away, when present scarcely differentiated from the rest of the spire but a little smoother (*Blanfordia integra*). Aperture broadly ovate, peristome dark-edged, usually thicker behind the edge and usually reenforced with a callus behind the outer lip. There is considerable variation in the strength of these characters, not only in the different species of the genus, but in the shells of individual species themselves; in *Blanfordia integra* the thickenings are merely indicated. Base narrowly umbilicated.

*Operculum*.—The operculum is thin, horny, paucispiral, that is, it consists of 2.2 whorls, the nucleus of which is not very excentric.

*Radula*.—The radula, like the shell, is larger in *Blanfordia* than in the other genera. The rachidian tooth has 5 denticles, a large median with a smaller one adjacent to this and the outer still smaller. In worn parts of the radula the latter is sometimes lost, but a search for it in less worn parts will always reveal it. The basals in the rachidian tooth are 4 on each side; the formula thus becomes  $\frac{2-1-2}{4-4}$ .

The lateral tooth is very oblique with 2 denticles inside of the large cusp and 3 or 4 on the outside of this. The first marginal bears 7-8 denticles. The outer marginal tooth has a thumblike projection on the inner end of the row of denticles. The denticles vary from 6 to 7. A glimpse at plate 3, figures 4-7, will give a better understanding of these features than does my description.

*Animal*.—I have not seen living *Blanfordias*. Adams (2) says of them, *i. e.*, *Blanfordia japonica* and *Blanfordia bensoni* A. Adams:

The tentacles are short and triangular; \* \* \* the eyes are sessile on the upper bases of the tentacles. \* \* \* The foot \* \* [is] lobed on each side in front and with a posterior dorsal lobe which bears the operculum. Both my species are found on damp banks covered with vegetation, in rocky situations near the sea.

I have copied Adams' figures of both species. To this Annandale (31) adds:

The snout is much longer and relatively narrower than that of *Oncomelania* and is highly extensile, forming a regular proboscis, while the foot is divided by a transverse furrow into two parts, which are capable of independent movement. The snail, instead of gliding evenly on its foot, moves something like a leech, dragging itself forward by means of its snout, the tip of which is applied to the ground, and pressing down the two parts of its foot separately.

## KEY TO THE SPECIES OF THE GENUS BLANFORDIA

Incremental sculpture consisting of closely spaced, well defined threads. . . . .*integra*.

Incremental sculpture not consisting of closely spaced, well defined threads.

Outer lip reenforced by a heavy varicial callus. . . . .*japonica*.

Outer lip not reinforced by a heavy varicial callus.

Callus of the outer lip merely indicated.

Shell large; height more than 7.5 mm. . . . .*bensoni*.

Shell smaller; height less than 7.0 mm. . . . .*simplex*.

## BLANFORDIA INTEGRA Pilsbry

Plate 1, fig. 12; plate 2, fig. 2; plate 3, fig. 4

1924. *Blanfordia integra* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 76, p. 12, fig. 3.

Shell small, very broadly ovate, thin, semitranslucent, horn-colored with the outer edge of the peristome bounded by a narrow, very dark brown zone; interior of the aperture of the same color as the exterior. Nuclear whorls 2.2, inflated, strongly rounded, very finely granulose when viewed under high magnification, forming a rather blunt apex. Postnuclear whorls 2.9 in the specimen figured, strongly inflated. The first turn at its junction with the nuclear whorl marked by almost axial riblets, which slant retractorily and which gradually become lessened in strength and on the last turn appear as fine axial threads, which are about as wide as the spaces that separate them. These whorls are also marked by faintly incised spiral lines which give to the surface an obscurely granulose effect when viewed under high magnification. Suture strongly constricted. Periphery inflated, strongly rounded. Base inflated, strongly rounded, moderately openly umbilicated, having the same sculpture as the spire covering it and extending into the umbilicus. Aperture large, very broadly obliquely ovate; peristome somewhat expanded all around and adnate at the parietal wall to the preceding whorl. Operculum thin with 2.2 whorls. In the radula the rachidian tooth has a strong median cusp bordered by two lesser cusps which decrease regularly in size outwardly. The basals are 4 in number and also decrease regularly outwardly, the formula for this, therefore, being  $\frac{2-1-2}{4-4}$ . The lateral tooth is very oblique with a very strong cusp and 2 minute cusps on the inside of this and 4 on the outside, the outer one being extremely small. The first marginal bears 7 denticles which decrease in size from the innermost outwardly. The outer marginal has 6 denticles with a seventh one indicated on the thumblike projection on the inside of the denticulated end.

Three specimens of this species, the type and two paratypes, are before me. They belong to the Philadelphia Academy of Natural Sciences, bearing the catalogue number 95757, and were collected by Y. Hirase in 1908 at Makuragisan, Izumo, Japan. They measure:

No. of whorls	Height in mm	Diameter in mm
5.0 <sup>a</sup>	4.6	3.0 (type)
5.3	5.2	3.2
4.5	3.6	2.4

<sup>a</sup> The type, whose shell, operculum, and radula I have figured.

The small size and strong axial sculpture easily distinguish this species from the other *Blanfordias*.

### BLANFORDIA JAPONICA (A. Adams)

Plate 1, figs. 11, 14 (type); plate 2, fig. 1; plate 3, fig. 5; plate 6, fig. 2

1861. *Tomichia japonica* A. ADAMS, Ann. Mag. Nat. Hist., ser. 3, vol. 8, p. 308.  
 1863. *Blanfordia japonica* A. ADAMS, Ann. Mag. Nat. Hist., ser. 3, vol. 12, p. 424, pl. 7, fig. 12.  
 1876. *Blanfordia japonica* PFEIFFER, Mon. Pneumon. Viv., pt. 4, p. 22.  
 1878. *Blanfordia japonica* NEVILL, Hand List Moll. Ind. Mus., pt. 1, p. 254.  
 1900. *Blanfordia japonica* MÖLLENDORFF, Nachrichtsbl. Deutsch. Malakoz. Ges., vol. 32, pp. 153-154.  
 1901. *Blanfordia bensoni minor* PILSBRY, Ann. Mag. Nat. Hist., ser. 7, vol. 8, p. 6.  
 1902. *Blanfordia japonica* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 54, pp. 26-27.  
 1903. *Blanfordia japonica* PILSBRY, Nautilus, vol. 16, p. 114.  
 1906. *Blanfordia japonica* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 58, p. 751.  
 1915. *Blanfordia japonica* PILSBRY, Nautilus, vol. 29, p. 2, figs. 1, 1a.  
 1924. *Blanfordia pilsbryana* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 290.  
 1924. *Blanfordia japonica* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 286, 288-291, text fig. 6c.  
 1929. *Blanfordia japonica* THIELE, Handb. Syst. Weicht., pt. 1, p. 150.  
 1934. *Blanfordia japonica* PILSBRY, Journ. Parasit., vol. 20, pp. 282-283.  
 1934. *Tomichia japonica* BEQUAERT, Journ. Parasit., vol. 20, p. 282.  
 1934. *Blanfordia pilsbryana* PILSBRY, Journ. Parasit., vol. 20, p. 283.

Shell of medium size, elongate-ovate, rather stout, horn-colored, with the outer edge of the peristome bounded by a narrow zone of dark chocolate brown. Interior of the aperture pale yellowish. The early whorls of all our specimens, except one, are decollated and the decollation is closed with a plug. In this specimen, which is in lot U.S.N.M. no. 346038, 2.2 whorls are present, but they are so



badly worn that no remarks about their sculpture can be made. Furthermore, part is broken away to show that a plug has already been formed in the interior, indicating where decollation is to take place. The remaining whorls are inflated and strongly rounded and are crossed by incremental lines of varying strength, some of which, not regularly spaced, assume almost the strength of threads. In addition to these, more or less regularly distributed incised microscopic spiral lines and obsolete lirations are present. Suture strongly constricted; periphery inflated and well rounded; base narrowly umbilicated, having the same sculpture as the spire. The last whorl is provided with a very heavy callus, slightly behind the peristome, which might be called a varix. Aperture very oblique, irregularly ovate, expanded at the outer edge and appressed and adnate to the base of the preceding turn at the parietal wall. The operculum is thin, horny, and has 2.2 whorls. In the radula the rachidian tooth has a strong median cusp, a lesser one adjoining this and a feeble one outside of it. The basals are 4 in number on each side and decrease in size from the inner outwardly, the outer one being poorly developed, the formula being  $\frac{2-1-2}{4-4}$ . The lateral has a very large cusp and 2 lesser ones on the inside of this, and 4 on the outside, the fourth being feebly developed. The inner marginal bears 7 denticles and the outer 6.

Adams' type, U.S.N.M. no. 21188, measures: Height, 7.1 mm, diameter, 4.2 mm. This has the outer lip partly fractured. I have therefore, in addition to this, figured another typical specimen from the type locality, U.S.N.M. no. 175797, which has 4.3 whorls remaining and measures: Height, 7.2 mm, diameter, 4.6 mm.

The additional specimens in our collection yield the following measurements:

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 21188.....	4.3	7.1	4.2 (type)
U.S.N.M. no. 175797.....	4.3 <sup>a</sup>	7.2	4.6
	4.3	7.2	4.6
	4.5	7.9	4.6
	4.5	7.6	4.6
	3.8	7.0	4.6
	4.2	7.1	4.4
	3.8	6.4	4.0



	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 346038.....	4.2	7.3	4.8 (type)
	3.4 <sup>a</sup>	7.4	4.4
	3.7	6.7	4.3
	4.3	6.8	3.9
	4.0	6.3	3.8
	4.0	6.6	4.2
	4.0	6.2	4.1
	3.7	6.7	4.3
	5.7 <sup>b</sup>	6.5	3.8
U.S.N.M. no. 307810.....	4.7	7.8	4.7
	4.3	7.3	4.8
	4.3	7.2	4.2
	4.4	7.4	4.6
	4.4	6.9	4.3
U.S.N.M. no. 307811.....	4.6	7.3	4.3
	4.5	8.0	4.8
	4.6	7.9	4.7
	4.3	7.4	4.5
	4.3	7.2	4.7
	4.5	7.4	4.5
Greatest .....	5.7	8.0	4.8
Least .....	3.7	6.2	3.8
Average .....	4.3 <sup>2</sup>	7.14	4.4

<sup>a</sup> Figured specimen.<sup>b</sup> Apex entire.

This species is easily differentiated from all the other *Blanfordias* by its very strong, varix-like callus behind the outer lip.

#### BLANFORDIA BENSONI (A. Adams)

Plate 1, fig. 13; plate 2, fig. 3; plate 3, fig. 7; plate 6, fig. 3

1861. *Tomichia bensoni* A. ADAMS, Ann. Mag. Nat. Hist., ser. 3, vol. 8, p. 308.  
 1863. *Blanfordia bensoni* A. ADAMS, Ann. Mag. Nat. Hist., ser. 3, vol. 12, p. 424,  
 pl. 7, fig. 11.  
 1876. *Blanfordia bensoni* PFEIFFER, Mon. Pneumon. Viv., pt. 4, p. 22.  
 1878. *Blanfordia bensoni* NEVILL, Hand List Moll. Ind. Mus., pt. 1, p. 254.  
 1897. *Blanfordia bensoni* MÖLLENDORFF, Nachrichtsbl. Deutsch. Malakoz. Ges.,  
 vol. 29, p. 32.  
 1900. *Pomatiopsis hirsaci* PILSBRY, Nautilus, vol. 14, p. 12.  
 1900. *Blanfordia bensoni* MÖLLENDORFF, Nachrichtsbl. Deutsch. Malakoz. Ges.,  
 vol. 32, p. 153.  
 1901. *Pomatiopsis hirsaci* PILSBRY, Ann. Mag. Nat. Hist., ser. 7, vol. 8, p. 5.  
 1901. *Blanfordia bensoni* PILSBRY, Ann. Mag. Nat. Hist., ser. 7, vol. 8, p. 5.  
 1902. *Blanfordia bensoni* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 54,  
 pp. 26-27.

1915. *Blanfordia bensoni* PILSBRY, Nautilus, vol. 29, p. 2, fig. 4.  
 1924. *Pomatiopsis hirasei* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 76, p. 12.  
 1924. *Pomatiopsis bensoni* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 76, p. 13.  
 1924. *Blanfordia bensoni* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 288-291, fig. 13.  
 1924. *Blanfordia bensoni hirasei* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 291-293, text fig. 6B.  
 1929. *Blanfordia (Vicina) bensoni* THIELE, Handb. Syst. Weicht., pt. 1, p. 150.  
 1934. *Blanfordia bensoni* PILSBRY, Journ. Parasit., vol. 20, pp. 281-283.  
 1934. *Blanfordia hirasei* PILSBRY, Journ. Parasit., vol. 20, p. 283.  
 1934. *Tomichia bensoni* BEQUAERT, Journ. Parasit., vol. 20, p. 281.

Shell large, elongate-ovate, moderately thick, light horn-colored with the outer edge of the peristomes chestnut brown. Interior of aperture a little lighter than the outside. The nuclear whorls in all of our specimens are decollated. The postnuclear whorls are inflated and strongly rounded and marked by moderately strong incremental lines which at irregular intervals develop into axial threads, probably marking resting stages in the growth. In addition to this, the whorls are marked by microscopic incised spiral lines and distantly placed, poorly and irregularly developed spiral lirations. All these sculptural elements are less strongly developed in the early postnuclear turns and gain slightly in strength as the shell increases in size. Suture strongly impressed; periphery and base inflated and strongly rounded, and marked with the same sculpture that characterizes the spire. The base is narrowly umbilicated. Aperture very broadly irregularly ovate; peristome slightly expanded and appressed and adnate to the preceding turn on the parietal wall. The operculum has 2.2 whorls. The radula is large and the rachidian tooth has a strong median cusp with 2 lesser cusps on each side and 4 basals on each side that decrease in size from the inner outward, the formula therefore being  $\frac{2-1-2}{4-4}$ . The lateral tooth is very oblique and has a powerful cusp with 2 lesser cusps on the inside of this and 3 on the outside. The first marginal bears 7 denticulations, and the outer marginal has 5.

The United States National Museum has three lots of this species, all collected by Y. Hirase in the southern end of the island of Hokkaido, as follows:

U.S.N.M. no. 307812, seven specimens from Ojima. Of one of these, we have given the figure of the shell, radula, and operculum.

A second lot, U.S.N.M. no. 162602, six specimens from Shikunobe, Ojima.

The last lot, U.S.N.M. no. 346036, 15 specimens from Ojima. These yield the following measurements:

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 307812.....	4.8 <sup>a</sup>	9.7	5.4
	4.6	9.2	5.3
	4.5	8.1	5.1
	4.4	8.6	5.1
	4.5	8.1	5.0
	4.5	8.0	4.8
	4.3	8.2	4.9
U.S.N.M. no. 162602.....	5.1	9.0	5.2
	4.4	8.7	4.9
	4.5	8.2	5.0
	4.5	7.9	4.8
	4.4	7.7	5.1
	4.5	8.3	4.8
U.S.N.M. no. 346036.....	4.7	9.2	5.7
	4.6	8.9	5.1
	4.6	9.1	5.3
	4.7	9.0	5.0
	4.6	8.6	5.1
	4.7	8.4	4.9
	4.7	8.8	5.3
	4.7	8.5	5.0
	4.5	8.5	5.0
	4.5	8.2	5.1
	4.4	7.9	5.0
	4.6	7.9	4.6
	4.4	8.0	5.1
	4.6	7.8	4.7
Greatest .....	5.1	9.7	5.7
Least .....	4.3	7.7	4.6
Average .....	4.58	8.46	5.05

<sup>a</sup> Shell, operculum, and radula figured.

In the measurements that we are citing, it should be borne in mind that the early whorls have been lost and the measurements are of the whorls remaining.

The large size of this species will easily distinguish it from the other *Blanfordias*.

## BLANFORDIA SIMPLEX Pilsbry

Plate 1, fig. 10; plate 2, fig. 4; plate 3, fig. 6

1902. *Blanfordia japonica* var. *simplex* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 54, pp. 26-27.
1903. *Blanfordia simplex* PILSBRY, Nautilus, vol. 16, p. 114.
1915. *Blanfordia simplex* PILSBRY, Nautilus, vol. 29, p. 2, figs. 3, 3a.
1924. *Blanfordia simplex* PILSBRY, Proc. Acad. Nat. Sci. Philadelphia, vol. 76, p. 13.
1924. *Blanfordia japonica simplex* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 291.
1934. *Blanfordia bensoni* PILSBRY, Journ. Parasit., vol. 20, p. 283.
1934. *Blanfordia bensoni simplex* PILSBRY, Journ. Parasit., vol. 20, p. 283.

Shell of medium size, ovate, thin, semitranslucent, pale horn-colored with the peristome bounded by a very narrow zone of chocolate brown; interior of aperture a little paler than the outside. Part of the nuclear spire is decollated, the portion remaining so cleverly plugged that one might be misled into taking it for the apex of the nucleus. The remaining turn is marked by fine granulations apparent only under high magnification. Postnuclear whorls strongly inflated, well rounded, marked by slender, depressed, threadlike incremental lines which are about as wide as the spaces that separate them, and microscopic spiral striations. Suture strongly constricted; periphery and base of the last whorl decidedly inflated and strongly rounded. The latter is marked like the spire. The base is narrowly umbilicated. Aperture oblique, oval with the peristome slightly expanded and appressed and adnate to the preceding turn at the parietal wall.

There are four lots before us, all collected by Y. Hirase. The specimen described and figured, U.S.N.M. no. 346042, is one of seven and comes from Uzen, Japan.

U.S.N.M. no. 346041, nine specimens from Noto, Japan.

U.S.N.M. no. 307809, six specimens from Nishigo, Uzen, Japan.

U.S.N.M. no. 162601, six specimens from Nishigo, Uzen, Japan.

They yield the following measurements:

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 346042.....	4.6 <sup>a</sup>	6.3	3.9
	4.5	6.3	3.9
	5.1	6.8	4.2
	4.7	6.5	3.9
	4.4	6.4	4.0
	4.3	6.5	4.1
	4.2	6.2	4.2

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 346041.....	4.5	6.6	3.9
	4.5	6.8	4.1
	4.5	6.8	4.2
	4.4	6.7	3.9
	4.5	6.5	3.9
	4.3	6.1	3.9
	4.6	6.9	4.0
	4.1	6.3	3.9
	4.4	6.6	4.2
U.S.N.M. no. 307809.....	4.4	6.0	3.8
	4.3	6.1	3.4
	4.5	5.9	3.8
	4.4	6.2	3.9
	4.5	6.6	4.1
	4.3	6.1	3.7
U.S.N.M. no. 162601.....	4.5	6.0	3.8
	4.7	6.7	4.2
	4.4	6.4	4.0
	4.3	6.2	4.0
	4.5	6.4	3.9
	4.4	6.0	3.9
Greatest .....	5.1	6.9	4.2
Least .....	4.1	5.9	3.7
Average .....	4.46	6.39	3.97

<sup>a</sup> Figured specimen.

### KATAYAMA

*Genotype*.—*Katayama nosophora* Robson.

Human schistosomiasis, its cause, and the life history of the organisms responsible for it furnish a fascinating chapter in the history of medicine, parasitology, and malacology. No other group of helminths yield the same stimulus to the historian—in fact, of all human parasites malaria alone furnishes a comparable theme. However, it is not within the scope of the present paper to elucidate this, but to render better known the mollusks constituting the key point for the control of the malady produced by the Asiatic blood fluke.

Probably no other small group of mollusks has met with more vicissitudes as far as the nomenclatorial problems are concerned than the members of the genus *Katayama*, and it is to be hoped that this effort will allay further changes and result in permanent names. This is especially desirable since the mollusks in question receive more attention in the medical than in the malacological press, and medical

men unskilled in molluscan lore must of necessity be puzzled, to say the least, about the names that should be applied to what they would term their pests. A perusal of the subjoined historical chapter of this genus, in which only the malacological side dealing with problems of naming has been cited, will explain past troubles.

#### HISTORY

From 1852, when Bilharz described *Distomum haematobium*, the African blood fluke, until 1913, only surmises were available about the probable life history of blood flukes.

The first intermediate host of *Schistosoma japonicum* to be described hailed from Rono in the center of the southern part of the Island of Formosa. It was christened *Blanfordia formosana* by Pilsbry (17, p. 751).

In 1913 Miyairi (19) announced a molluscan intermediate host for the Asiatic blood fluke. This immediately set into action with renewed energy research students in various parts of the world.

The year following, 1914, Miyairi and Suzuki (20) published their paper on "Der Zwischenwirt des *Schistosomum japonicum* Katsurada."

In 1915 Leiper and Atkinson (21) published "Observations on the Spread of Asiatic Schistosomiasis", in which they give an account of their search for the intermediate host in China and Japan.

By far the greatest impetus to an understanding of this genus was furnished by Robson (22), who in 1915 described as a new genus and new species *Katayama nosophora*, the then known intermediate host of *Schistosoma japonicum*.

Pilsbry (23) in the same year refers this to the genus *Blanfordia*. He also lists under this species the shells which I have here named *Katayama nosophora yoshidai*.

In 1918 Johnson (24), in reviewing "The Cercarian Infection of South African Snails", by F. G. Cawston, M.D., refers to *Blanfordia* (*Katayama*) *nosophora*.

The following year, 1919, Cort (25) published a paper on "The Cercaria of the Japanese Blood Fluke, *Schistosoma japonicum* Katsurada", and gives an account of its intermediate host, *Blanfordia nosophora*.

The year following, 1920, Cort (26) published a paper "On the Resistance to Desiccation of the Intermediate Host of *Schistosoma japonicum* Katsurada."

The form here used appears to be my *Katayama nosophora yoshidai*.

In 1921 Cort (28) published a splendid paper on "The Development of the Japanese Blood Fluke, *Schistosoma japonicum* Katsurada, in Its Final Host" and names as such *Blanfordia nosophora*. The mollusks he says were received from Sado Yoshida of the Osaka Medical College and were most likely my subspecies *Katayama nosophora yoshidai* received from the same source.

The same year Robson (27) published his exhaustive and splendid study "On the Anatomy and Affinities of *Hypsobia nosophora*", i. e., the mollusks he had in 1915 named *Katayama nosophora*.

In 1923 Meleney and Faust (29) published a paper on "The Intermediate Host of *Schistosoma japonicum* in China" and here cite *Blanfordia nosophora* and also an *Oncomelanian*.

The next year, 1924, Faust (33) again discusses the problem in his paper entitled "Notes on Larval Flukes from China. II. Studies on Some Larval Flukes from the Central and South Coast Provinces of China." He states here (p. 243) that the cercaria of *Schistosoma japonicum* were found at Shaohsing in *Katayama nosophora*; this is the mollusk I named *Katayama fausti* the following year. He properly places *Katayama nosophora* and *Katayama formosana* in their correct genus and exonerates the *Blanfordias* from being schistosomophorous. He proclaims the *Katayamas* as mountain dwellers and the *Oncomelantias* as occupying the Yangtze delta and Grand Canal and Great Lake. These he also proclaims schistosomophorous.

The same year Annandale's (31) paper on "The Molluscan Hosts of the Human Blood Fluke in China and Japan, and Species Liable to be Confused with Them" appeared. This was an extensive study, in which he definitely eliminated *Blanfordia* as a carrier, but, reduced *Katayama* to a section of *Oncomelania*, which he called *Katayamae*. In this he placed *Oncomelania formosana* and *Oncomelania nosophora*. His treatment of *Oncomelania* I shall discuss under that genus. He discussed classification at considerable length.

In 1925 Bartsch (35) bestowed names upon three *Katayamas*: *Katayama nosophora yoshidai* from Kurume, Kyushu Island, Japan; *Katayama fausti* from Shaohsing, Chekiang Province, China; and *Katayama fausti cantoni* from Fatshan near Canton, China. He also discussed *Katayama nosophora* and *Oncomelania*.

In 1926 Germain and Neveu-Lemaire (36), in their "Essai de Malacologie Medicale", discuss the mollusks playing a part as intermediate hosts. They recognize *Oncomelania* as a genus and *Hypsobia* and *Hemibia* as sections thereof. The latter we have pointed out previously is a pure and simple synonym of *Oncomelania* with the same type, while the former is completely excluded from *Oncomelania*.



by its anatomic characters. *Katayama* they consider synonymous with *Oncomelania*; under it they list *Oncomelania (Hypsobia) nosophora* and *Oncomelania (Hypsobia) formosana*. They also refer under *Oncomelania (Hypsobia) nosophora* Faust's specimens from Shaohsing and Fatshan, which I have named *Katayama fausti* and *Katayama cantoni*, respectively.

In 1928 Bequaert (37) published his essay on "Mollusks of Importance in Human and Veterinary Medicine." In this he reviews the entire field and places the *Katayamas* in *Oncomelania*. He lists *Blanfordia nosophora* and *Blanfordia formosana* as hosts of our fluke.

In 1929 Faust (39) published his textbook, "Human Helminthology", in which he discusses schistosomiasis on pages 94-155.

In 1932 Tubangui (40) announced "The Molluscan Intermediate Host in the Philippines of the Oriental Blood Fluke, *Schistosoma japonicum* Katsurada", in which he refers to *Blanfordia japonica* and *Blanfordia formosana*.

The same year, 1932, Rensch (41) in describing the Philippine intermediate host of *Schistosoma*, refers to *Hypsobia nosophora*.

In 1932 Fu-ching Li published two papers in Science, The Science Society of China, vol. 16. The first of these (42), pp. 566-582, deals with der "Zwischenwirt des *Schistosomum haematobium japonicum* (Katsurada)"; the second (43) in the same journal, pp. 583-619, deals with "Über die postembryonale Entwicklung von dem Zwischenwirt des *Schistosomum haematobium japonicum* China." This contains 32 figures. It is unfortunate that both of these papers are in Chinese, but in a subsequent paper (46), 1934, the author uses German, so we may consider that the data here presented is summed up in that communication.

In 1934 Bequaert (44) reviews Tubangui and Rensch's papers and incidentally goes over all the ground again, referring to *Blanfordia formosana* and *Katayama nosophora*.

To the same paper Pilsbry (45) adds an appendix, "Note on the Genus *Blanfordia*", in which he substantiates Bequaert's conclusion and refers, among other things, to *Katayama nosophora yoshidai* and *Blanfordia nosophora*.

#### GENERIC DEFINITION

*Shell*.—Shell elongate-conic or very elongate-ovate, thin, semi-transparent, horn-colored with a dark line marking the edge of the peristome. Nuclear whorls well rounded, smooth, under very high

magnification minutely granulose. Postnuclear whorls moderately to well rounded, marked with incremental lines that vary in strength and spacing. Suture varying from moderately to strongly constricted. Periphery and base well rounded, base narrowly umbilicated. Outer lip provided with a callus behind the aperture. Aperture broadly ovate.

*Operculum*.—The operculum is thin, horny, paucispiral, consisting of 3.2 whorls, with the nucleus somewhat excentric.

*Radula*.—The radula is moderately large. The rachidian tooth has 3 denticles, *i. e.*, a large median and a lesser one flanking this on each side. The basal denticles in the rachidian tooth are 3 on each side; the formula therefore is  $\frac{1-1-1}{3-3}$ . The lateral tooth is very oblique, bearing 6 denticles, of which the third from the inner edge is a giant compared to the rest. The inner marginal tooth varies in the number of denticles in the different species, from 7 to 9. The number of denticles in the outer marginal tooth range from 5 to 7, the innermost being much larger than the rest. In this character the *Katayamas* are also distinguished from the *Blanfordias*.

*Animal*.—I have not studied these animals alive; all the information here cited is therefore second-hand.

The anatomy of the alimentary, respiratory, renal, circulatory, nervous and reproductive systems is beautifully described and figured by Robson (27). The affinities of the animal are also worked out by him. To this masterly paper we refer any one interested in these subjects.

*The egg*.—The eggs, Dr. Li writes me, "are attached as individual specimens to rocks and are covered with sand." His figure here published (pl. 6, fig. 4) also shows five side by side in chain formation. In *Oncomelania* they form clumps enclosed in a common jelly mass.

*Ecology*.—Robson, quoting Leiper, says that they (*Katayama nosophora*) "occur in damp moss and grass on the sides of plants in the rice fields in very great quantities."

Li, as well as Faust and Meleney, found the Chinese species to be mountain dwellers. A glimpse at an Eastern Chinese topographic map shows that the mountain range attains a height of 4,000 feet at a moderate distance from shore along the coast, and it is in the streams of this that *Katayama* finds a suitable habitat. Of the habits of *Katayama fausti* Faust (32) states:

[At] the village of Ch'en Chia Chiao, about three and a half miles from the southwest corner of Shaohsing City, \* \* on the intermediate ground of moist

humus and moss numerous specimens of a snail, recognized as a *Katayama*, were found. \* \* \* The specimens collected were all taken from mossy banks or underneath the moss in the porous humus or loose wet mud. Both living snails and dead shells were found in this locality, but in the clay banks above the stone bridge, where there was no moss, the *Katayamas* were absent.

Of *Katayama cantoni*, Faust (32) states:

In the village of Tip Kan [Island of Honam], about one mile from Fatshan, the banks of a secondary stream were covered at high water level with moss and loose moist humus. Careful search at this point revealed numerous specimens of *Katayama*.

Dr. Li gives an interesting discussion on the ecology and geographical distribution of these forms based upon personal field studies, which students will find fertile reading.

All the species here discussed are schistosomophorous. The Chinese *Katayama fausti* and *Katayama cantoni* were first so implicated by Faust and Meleney. *Katayama lii* was found also by Dr. Li to serve as intermediate host.

#### KEY TO THE SHELLS OF THE SPECIES OF THE GENUS KATAYAMA

Shell elongate-ovate ..... *formosana*.  
Shell not elongate-ovate.

Shell elongate-conic.

Shell rather slender, obsolete threadlike axial sculpture fine, closely spaced.

Average measurements of complete shell:

No. whorls 7.6; height 6.4 mm; diam. 2.8 mm. .... *nosophora*.

No. whorls 8.6; height 7.5 mm; diam. 3.1 mm. .... *n. yoshidai*.

Shell rather stout, obsolete threadlike axial sculpture coarse and more distantly spaced.

Shell large; height more than 7.7 mm. .... *lii*.

Shell smaller; height not more than 6.6 mm.

Shell rather coarse. .... *fausti*.

Shell rather delicate. .... *cantoni*.

#### SYNOPSIS OF THE NUMBER OF DENTICULATIONS ON THE MARGINAL TEETH OF THE SPECIES OF KATAYAMA

1st marginal	2d marginal	Species
9	7	<i>lii</i>
9	6	<i>nosophora</i>
9	5	<i>formosana</i>
8	6	<i>yoshidai</i>
8	5	<i>fausti</i>
7	5	<i>cantoni</i>

## KATAYAMA NOSOPHORA NOSOPHORA Robson

Plate 1, fig. 4; plate 2, fig. 8; plate 4, fig. 1

1913. Description of Intermediate Host of *Schistosoma japonicum* MIYAIRI, K. Tokio Med. Weekly, no. 1839.
1914. Der Zwischenwirt des *Schistosoma japonicum* MIYAIRI and SUZUKI, Mitt. Med. Fak. Kais. Univ. Kyushu, vol. 1, pp. 187-197, pls. 1-2.
1915. *Katayama nosophora* ROBSON, Brit. Med. Journ., Jan. 1915, p. 203, figs. 7-9, 11.
1915. *Blanfordia nosophora* PILSBRY, Nautilus, vol. 29, pp. 1-4, figs. 2, 2a.
1918. *Blanfordia (Katayama) nosophora* JOHNSON, Nautilus, vol. 31, p. 141.
1919. *Blanfordia nosophora* CORT, Univ. California Publ., vol. 18, pp. 485-507.
1920. *Blanfordia nosophora* CORT, Journ. Parasit., vol. 6, pp. 84-88.
1921. *Hypsobia nosophora* ROBSON, Ann. Mag. Nat. Hist., ser. 9, vol. 8, pp. 401-413, figs. 1-7.
1921. *Katayama nosophora* ROBSON, Ann. Mag. Nat. Hist., ser. 9, vol. 8, p. 402.
1921. *Blanfordia nosophora* CORT, Amer. Journ. Hyg., vol. 1, pp. 1-38.
1924. *Oncomelania nosophora* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 283-284, 286, 289, 290, pl. 36, figs. 6-8.
1924. *Katayama nosophora* FAUST, Amer. Journ. Hyg., vol. 4, p. 269.
1925. *Katayama nosophora* BARTSCH, Journ. Washington Acad. Sci., vol. 15, p. 71.
1926. *Oncomelania (Hypsobia) nosophora* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, p. 293, fig. 1.
1928. *Blanfordia nosophora* BEQUAERT, Amer. Journ. Trop. Med., vol. 8, p. 225.
1929. *Katayama nosophora* FAUST, Human Helminthology, p. 136, fig. 47a.
1932. *Blanfordia nosophora* TUBANGUI, Philippine Journ. Sci., vol. 49, p. 299.
1932. *Hypsobia nosophora* RENSCH, Philippine Journ. Sci., vol. 49, p. 552.
1934. *Blanfordia nosophora* PILSBRY, Journ. Parasit., vol. 20, pp. 283-284.
1934. *Katayama nosophora* PILSBRY, Journ. Parasit., vol. 20, p. 284.
1934. *Katayama nosophora* BEQUAERT, Journ. Parasit., vol. 20, p. 282.

Shell elongate-conic, thin, horn-colored with the outer edge of the peristome marked by a dark chocolate line. Nuclear whorls 2.1, well rounded, smooth except for exceedingly minute microscopic granulations, which are apparent only under very high magnification. The nuclear spire terminates rather bluntly. Postnuclear whorls moderately well rounded, marked by fine incremental lines which might be called obsolete, closely spaced, slender axial threads. Suture rather strongly constricted; periphery of the last whorl well rounded. Base moderately long, narrowly umbilicated, well rounded and marked by a continuation of the incremental sculpture referred to above. The base is not thickened at the columella as it is in the Chinese species, but remains comparatively slender. The last whorl is thickened into a moderately strong callus behind the edge of the peristome. Aperture broadly ovate; peristome slightly expanded and reflected. Parietal wall adnate to the preceding turn. Operculum thin, horny, paucispiral, consisting of 3.2 whorls with the nucleus excentric.

This subspecies differs from *Katayama nosophora yoshidai* in being smaller in every way and in having an additional denticle on the inner marginal tooth.

We have seen three lots, 60 specimens, of this race. The first, U.S.N.M. no. 346040, 9 specimens, collected by Y. Hirase comes from Katayama, Bingo Province, Honshu Island, Japan, the type locality of *Katayama nosophora nosophora*.

U.S.N.M. no. 341076 contains 10 specimens from the same locality, collected by Dr. M. Miyajima.

U.S.N.M. no. 420948 contains 41 specimens collected by Dr. E. C. Faust at Okayama, Honshu Island, Japan, near the type locality. These yield the following measurements:

	No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 346040..	6.8 <sup>a</sup>	7.5	2.9	5.4	6.5	3.1
	6.4	7.1	2.9	6.3	7.6	3.2
	5.4	6.4	2.9	6.4	6.8	2.9
	6.1	6.5	2.6	5.5	5.8	2.8
	6.2	5.7	2.4	6.1	6.0	2.7
	5.3	6.6	3.1	5.8	5.8	2.7
	6.3	6.3	2.7	4.9	5.7	3.0
	6.0	5.8	2.4	5.7	5.9	2.7
	4.7	5.1	2.6	5.8	5.8	2.9
				5.2	5.4	2.4
U.S.N.M. no. 341076..	6.2	6.9	3.1	6.6	6.4	3.0
	5.5	7.0	3.4	6.3	5.8	2.6
	4.8	6.4	3.2	5.7	5.7	2.5
	5.4	6.8	3.3	4.7	5.2	2.6
	5.8	7.4	3.4	5.4	5.4	2.4
	7.5	7.5	3.3	5.7	6.3	2.9
	5.9	7.0	3.3	6.2	6.0	2.8
	5.2	6.5	3.2	6.4	7.1	3.1
	5.3	5.9	3.0	6.0	7.2	3.3
	5.1	5.8	2.9	6.3	6.5	2.9
				6.8	6.7	2.8
U.S.N.M. no. 420948..	5.6	6.5	3.1	5.3	6.8	3.2
	6.0	8.0	3.4	7.6	7.6	3.2
	5.5	6.2	2.7	6.7	7.0	3.1
	6.4	7.2	2.9	6.2	7.0	3.1
	7.5	6.4	2.8	6.8	7.5	3.2
	5.1	6.0	2.8	5.7	7.1	3.2
	6.8	7.4	3.0	8.0	8.6	3.3
	7.6	8.1	3.2	6.5	7.1	3.0
	6.8	7.7	3.4	5.7	7.5	3.4
	5.3	6.0	2.8	7.4	7.7	3.3
Greatest .....				8.0	8.6	3.4
Least .....				4.7	5.1	2.4
Average .....				6.03	6.62	2.97

<sup>a</sup> Figured specimen.

KATAYAMA NOSOPHORA YOSHIDAI Bartsch

Plate 1, fig. 1; plate 2, fig. 9; plate 4, fig. 2

1915. *Blanfordia nosophora* PILSBRY, Nautilus, vol. 29, p. 3, figs. 2, 2a.  
1920. ?*Blanfordia nosophora* CORT, Journ. Parasit., vol. 6, pp. 84-85.  
1921. ?*Blanfordia nosophora* CORT, Amer. Journ. Hyg., vol. 1, pp. 1-38.  
1924. *Katayama nosophora* FAUST and MELENEY, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 29-30; 34; 37-42; 82-83; 87.  
1924. *Oncomelania nosophora* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 284, in part.  
1925. *Katayama nosophora yoshidai* BARTSCH, Journ. Washington Acad. Sci., vol. 15, pp. 71-72.  
1929. *Katayama nosophora* FAUST, Human Helminthology, p. 136, in part.  
1934. *Katayama nosophora yoshidai* PILSBRY, Journ. Parasit., vol. 20, p. 283.  
1934. *Blanfordia nosophora* PILSBRY, Journ. Parasit., vol. 20, p. 283.

Shell in every way similar to *Katayama nosophora nosophora*, differing from it in being in every way a little larger and in having a different denticulation count in the inner marginal teeth. *Katayama nosophora yoshidai* has 8 denticles, and *Katayama nosophora nosophora* has 9.

The type and the 100 paratypes here measured were received from Dr. Yoshida and were collected at Kurume, Kyushu Island, Japan. The 100 paratypes whose measurements are subjoined here were not selected but taken at random.

Only the specimens marked with a superior b have the shell complete.

	No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 362024..	7.8 <sup>a</sup>	8.1	3.4	5.8	6.6	3.0
				5.7	6.8	3.0
U.S.N.M. no. 340953..	4.7	7.3	3.4	6.1	7.4	3.3
	6.3	7.4	3.3	5.2	6.7	3.3
	5.5	6.9	3.2	7.0	7.3	3.0
	5.7	6.8	3.1	6.0	6.8	3.1
	5.7	6.7	3.2	6.0	7.0	3.0
	5.8	6.3	2.8	5.6	6.4	2.9
	7.6	7.1	3.0	5.6	6.6	3.1
	6.0	7.3	3.0	6.2	6.8	3.1
	5.8	6.9	3.1	5.7	6.7	3.3
	8.7 <sup>b</sup>	8.2	3.2	5.2	6.0	2.8
	6.7	7.9	3.4	6.3	7.1	3.2
	6.1	7.2	3.0	6.1	7.1	3.1
	6.1	7.2	3.2	5.8	6.1	2.9
	5.7	6.1	2.9	7.5	7.1	3.0
	8.5 <sup>b</sup>	7.4	2.9	5.7	6.3	3.0
	7.1	6.4	2.9	5.7	6.3	2.9
	5.4	6.1	2.8	6.2	7.3	3.2
	5.7	6.8	3.1	6.5	7.9	3.4



	No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 340953..	6.3	6.6	2.9	7.1	7.3	3.1
	6.7	7.0	3.0	5.6	6.7	3.0
	5.4	6.1	3.0	5.6	6.4	2.8
	6.6	6.3	2.9	5.7	6.6	3.1
	7.7	7.7	3.1	8.5 <sup>b</sup>	7.8	3.4
	6.6	7.4	3.3	6.0	6.5	3.0
	6.1	7.2	3.1	6.3	7.1	3.3
	6.5	6.4	2.9	5.4	6.5	2.9
	6.1	7.0	3.0	6.6	7.9	3.4
	5.7	6.2	3.0	5.7	6.4	2.9
	6.2	7.2	3.4	6.0	7.3	3.2
	6.3	7.6	3.3	6.4	7.4	3.2
	6.2	6.4	2.8	5.8	6.6	3.0
	7.4	7.8	3.2	5.7	6.5	2.9
	6.1	6.7	3.0	5.6	6.4	2.9
	5.7	7.0	3.3	5.3	6.2	2.9
	6.3	7.1	3.1	5.8	5.7	2.7
	5.7	6.2	2.9	7.8 <sup>b</sup>	6.7	2.9
	6.0	7.1	3.2	6.0	6.3	2.8
	6.3	7.2	3.1	6.2	6.9	3.0
	6.1	6.5	3.0	6.1	7.5	3.3
	5.9	6.6	3.1	6.2	6.6	3.1
	5.7	7.2	3.4	5.5	6.8	3.0
	6.0	6.6	2.9	6.1	6.9	3.2
	6.0	6.7	2.8	6.2	7.1	3.2
	5.6	6.8	3.4	5.5	6.6	3.1
	5.7	7.0	3.1	6.0	7.3	3.2
	6.1	6.9	3.2	7.5	7.5	3.2
	6.0	7.4	3.1	5.4	6.1	2.8
	5.5	6.3	2.9	6.4	7.1	3.2
	5.3	5.8	2.8	6.3	6.8	3.2
Greatest .....				8.7	8.2	3.4
Least .....				4.7	5.7	2.7
Average .....				6.13	6.86	3.07

<sup>a</sup> Figured type.<sup>b</sup> Complete shell.**KATAYAMA FORMOSANA (Pilsbry and Hirase)**

Plate 1, fig. 6; plate 2, fig. 12; plate 4, fig. 3

1906. *Blanfordia formosana* PILSBRY and HIRASE, Proc. Acad. Nat. Sci. Philadelphia, vol. 57, pp. 750-751.
1924. *Katayama nosophora* FAUST and MELENEY, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 82.
1924. *Oncomelania formosana* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 284-286, 293, pl. 36, figs. 3-5.
1924. *Katayama formosana* FAUST, Amer. Journ. Hyg., vol. 4, p. 274.
1925. *Katayama formosana* BARTSCH, Journ. Washington Acad. Sci., vol. 15, p. 71.



1925. *Blanfordia formosana* BARTSCH, Journ. Washington Acad. Sci., vol. 15, p. 71.  
 1926. *Oncomelania (Hyphsobia) formosana* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, p. 294.  
 1928. *Blanfordia formosana* BEQUAERT, Amer. Journ. Trop. Med., vol. 8, p. 225.  
 1929. *Katayama formosana* FAUST, Human Helminthology, p. 136.  
 1932. *Blanfordia formosana* TUBANGUI, Philippine Journ. Sci., vol. 49, p. 299, pl. 2, fig. 4.  
 1934. *Blanfordia formosana* BEQUAERT, Journ. Parasit., vol. 20, p. 281.

Shell elongate-ovate, thin, semitranslucent, horn-colored, bordered by a chocolate-brown line. Interior of the aperture of the same color as the exterior. Nuclear whorls 2.0, well rounded, smooth, except for exceedingly fine microscopic granules, forming a rather blunt apex. Postnuclear whorls somewhat inflated, strongly rounded, and marked by slightly retractively curved incremental lines, which here and there assume the strength of obsolete threads. There are also obsolete spiral lirations present. Suture strongly impressed; periphery inflated, strongly rounded. Base rather short, strongly rounded, narrowly umbilicated and marked like the spire. The last whorl has a heavy callus behind the outer lip which extends to the columella. Aperture broadly ovate; outer lip thin, slightly reflected and adnate at the parietal wall to the preceding turn. Operculum thin, paucispiral, horny, consisting of 3.2 whorls with the nucleus excentric. The radula possesses the typical katayamid formula, that is  $\frac{1-1-1}{3-3}$ , for

the rachidian tooth. The lateral has likewise the typical rachidian formula of 6 denticles, with the third counting from the inside, much larger than the rest. The first marginal has 9 denticles and the outer marginal has 5 denticles with the innermost much larger than the rest.

The specimen described and figured, U.S.N.M. no. 307270, is one of several hundred specimens from Rono, Formosa. It has 7.2 whorls, and measures: Height, 6.5 mm; diameter, 3.4 mm.

A hundred additional specimens, U.S.N.M. no. 420941, yield the measurements given in the subjoined table.

	No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 307270..	7.2 <sup>a</sup>	6.5	3.4	6.7	5.5	3.0
				6.8	5.7	2.9
U.S.N.M. no. 420941..	6.8	5.5	2.9	6.4	4.8	2.5
	6.4	5.0	2.9	6.4	5.2	2.7
	6.5	5.3	2.8	6.3	4.7	2.5
	6.4	5.0	2.8	6.8	5.8	3.0
	6.5	5.6	3.2	6.3	5.3	2.9
	6.5	5.3	2.9	7.3	6.4	3.2
	7.2	5.9	2.9	6.8	5.3	2.7

	No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 420941..	7.0	5.8	3.1	6.5	4.9	2.5
	7.2	6.3	3.2	6.3	4.8	2.5
	6.4	5.7	3.1	6.4	5.2	2.7
	6.5	5.1	2.8	6.8	5.5	2.8
	6.4	4.7	2.5	6.6	5.5	2.9
	6.7	5.0	2.5	7.1	6.0	2.9
	6.6	5.2	2.8	6.6	5.5	2.8
	5.6	4.2	2.6	6.5	5.1	2.8
	6.3	4.8	2.7	6.6	5.4	3.0
	6.4	5.3	2.9	6.4	4.9	2.7
	6.8	5.4	2.9	6.8	5.2	2.7
	7.2	6.0	3.2	6.3	5.3	2.9
	7.0	5.8	3.0	6.7	5.3	2.8
	7.0	5.7	3.0	6.7	5.5	3.0
	6.5	5.2	2.7	6.7	5.6	3.0
	6.8	5.3	2.8	6.4	5.2	2.9
	6.5	5.0	2.8	6.6	5.5	3.1
	6.5	5.3	2.7	6.4	5.1	2.8
	7.0	5.8	3.2	6.6	5.2	2.8
	7.2	6.2	3.1	6.7	5.3	2.9
	7.2	5.6	2.8	6.3	4.9	2.5
	6.9	5.5	3.0	6.6	5.6	2.9
	6.8	5.9	3.2	6.5	5.0	2.6
	6.4	5.1	3.0	6.7	5.6	3.1
	6.4	5.2	2.9	7.2	6.1	3.0
	6.4	4.9	2.7	6.7	5.6	2.9
	6.7	5.5	2.8	6.9	5.9	2.9
	7.3	6.4	3.1	6.1	4.7	2.7
	6.7	5.6	2.9	6.0	4.5	2.5
	6.4	4.9	2.6	6.1	4.7	2.5
	6.6	5.6	3.0	6.8	5.5	2.9
	6.5	5.1	2.8	6.3	4.7	2.5
	7.1	6.2	3.2	6.5	4.8	2.5
	7.3	6.1	3.1	6.4	5.2	2.7
	6.8	5.6	2.9	6.6	5.4	2.9
	6.5	5.6	2.9	6.7	5.7	3.0
	7.0	5.8	3.1	6.4	5.0	2.6
	7.0	5.6	2.8	6.5	5.6	3.0
	6.3	4.8	2.6	6.4	5.2	2.8
	6.8	5.7	3.0	6.4	5.1	2.6
	7.0	5.6	2.8	6.4	4.9	2.7
	6.8	5.5	2.8	6.6	5.2	2.5
Greatest .....	7.3	6.4	3.2			
Least .....	5.6	4.2	2.5			
Average .....	6.63	5.37	2.84			

<sup>a</sup> Figured specimen.

This species can at once be distinguished from all the other *Katayamas* by its elongate-ovate shape.

## KATAYAMA LII, n. sp.

Plate 1, fig. 5; plate 2, fig. 11; plate 4, fig. 4; plate 6, figs. 4, 7

Shell elongate-conic, moderately heavy, horn-colored with a narrow chocolate-brown line edging the peristome. The interior of the aperture is the same as the exterior. Nuclear whorls 2.1, well rounded, smooth except for fine microscopic granulations. The postnuclear whorls are well rounded, marked by low, obsolete, threadlike incremental lines which are rather coarse and of varying size and spacing. Microscopic lirations are merely indicated as a spiral sculptural element. Suture moderately strongly constricted; periphery of the last whorl well rounded. Base well rounded, narrowly umbilicated, marked like the spire. There is an exceedingly strong callus behind the outer peristome, which extends over the columella and renders this rather thickened. Aperture broadly ovate, tending toward subquadrate. Peristome slightly expanded and reflected and adnate to the preceding whorl at the parietal wall. Operculum thin, horny, paucispiral, having 3.2 turns with the nucleus excentric. The radula has the typical rachidian tooth, that is,  $\frac{1-1-1}{3-3}$ . The lateral is likewise typically katayamid, having 6 denticles with the third from the inside much larger than the rest. The inner marginal bears 9 denticles and the outer 7.

The type, U.S.N.M. no. 420949, is a complete specimen with 8.5 whorls and measures: Height, 8.0 mm; diameter, 3.4 mm.

We have three additional specimens, U.S.N.M. no. 420942, which yield the following measurements. These were collected by Dr. Fuching Li, for whom the species is named, at Lin-an and Hiau-Fen, China, respectively.

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 420949.....	8.5 <sup>a</sup>	8.0	3.4 (type)
U.S.N.M. no. 420942.....	7.5	8.2	3.2
	8.7	8.2	3.4
	7.2	7.7	3.4

<sup>a</sup> Type specimen.

This species is most nearly related to the other two Chinese forms here described, but differs from them conspicuously in its larger size and the radular formula.

## KATAYAMA FAUSTI Bartsch

Plate 1, fig. 2; plate 2, fig. 10; plate 4, fig. 5

1924. *Oncomelania nosophora* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 283-284, in part, also p. 293.
1924. *Katayama nosophora* FAUST, Amer. Journ. Hyg., vol. 4, pp. 243, 269, 274.
1925. *Katayama fausti* BARTSCH, Journ. Washington Acad. Sci., vol. 15, pp. 71-72.
1926. *Oncomelania (Hypsobia) nosophora* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, p. 293, in part.
1929. *Katayama nosophora* FAUST, Human Helminthology, p. 136, in part.

Shell elongate-conic, brownish horn-colored. Nuclear whorls decollated in all our specimens. The postnuclear whorls, well rounded, marked by irregular, rather coarse, incremental lines, which might be interpreted as closely spaced obsolete riblets, which are best developed on the last turn. Suture strongly constricted; periphery well rounded. Base slightly prolonged, well rounded, marked by a continuation of the sculpture present on the spire, narrowly umbilicated. The last whorl is provided with a very heavy callus immediately behind the aperture, which extends over the base of the lip on to the columella, thickening this materially. The outer lip is slightly expanded and reflected and adnate to the preceding turn at the parietal wall. The operculum is thin, corneous, paucispiral with excentric nucleus. The radula has the formula  $\frac{1-1-1}{3-3}$ , 2-1-3 for the median, that is, two inner small teeth followed by a very large third and 3 small. The inner marginal has 8 denticles and the outer 5.

The type, U.S.N.M. no. 362025, as well as two additional specimens, U.S.N.M. no. 362026, were collected by Dr. E. C. Faust at Shaohing, Chekiang Province, China. They yield the following measurements:

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 362025.....	5.4 <sup>a</sup>	6.6	3.0
U.S.N.M. no. 362026.....	5.2	5.5	2.8
	4.7	6.5	3.2

<sup>a</sup> Figured type.

This species can readily be distinguished from *Katayama lii* by its smaller size and radular formula, and from *Katayama cantoni* by its radular formula and heavier coarser shell.

## KATAYAMA CANTONI Bartsch

Plate 1, fig. 3; plate 2, fig. 13; plate 4, fig. 6

1924. *Oncomelania nosophora* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 283-284, in part.
1925. *Katayama fausti cantoni* BARTSCH, Journ. Washington Acad. Sci., vol. 15, pp. 71-72.
1926. *Oncomelania (Hypsobia) nosophora* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, pp. 292-293, in part.

Shell elongate-conic, thin, semitranslucent, horn-colored, the outer lip bordered with a slightly darker edge. The early whorls eroded, those remaining well rounded and marked by obsolete incremental lines, and on the last whorl by indications of irregularly distantly spaced, axial threads. Suture constricted; periphery well rounded. Base well rounded, narrowly umbilicated and marked by the same sculpture that characterizes the spire. The last whorl has a little behind the aperture a moderately thick callus that extends over the base of the lip to the columella, which it somewhat thickens. Aperture ovate; outer lip slightly expanded and reflected and adnate to the preceding turn at the parietal wall. The operculum is thin, horn-colored, and paucispiral with 3.2 whorls, and has an excentric nucleus.

The radula has the typical rachidian tooth  $\frac{1-1-1}{3-3}$ . The lateral is also typical, 2-1-3, that is, 2 smaller inner denticles with a large third tooth followed by 3 lesser denticles. The inner marginal has 7 denticles, the outer 5.

The type, U.S.N.M. no. 362027, was collected by Dr. E. C. Faust at Fatshan, near Canton, China. It has 5.3 whorls and measures: Height, 6.4 mm; diameter, 2.8 mm.

An additional specimen, U.S.N.M. no. 362028, from the same source yields the following measurements: Height, 6.3 mm; diameter, 3.1 mm. It has 5.3 whorls.

This species, which we first considered a subspecies of *fausti*, is far removed from that by reduction of the denticles of the inner marginal tooth to 7. The shell also is thinner and more fragile.

## SCHISTOSOMOPHORA, n. gen.

*Genotype*.—*Prososthenia quadrasi* Möllendorff.

The discovery of the intermediate host of the Asiatic blood fluke in the southern Philippines by Tubangui made it desirable to investigate its relationship to the other schistosomophorous mollusks, with the result that although related to *Katayama* and *Oncomelania*, the

mollusks in question, nevertheless, are as different from each of these as these differ among themselves. It is for this reason that I propose the generic name *Schistosomophora* for them.

#### HISTORY

In 1895 von Möllendorff (10) described, among other minute operculates, *Prososthenia quadrasi* from near the town of Surigao, northeastern Mindanao, Philippine Islands. Little did he suspect the important role that this insignificant-looking snail would be found to play in the health of this region. We, therefore, find little beyond a mere listing of the species in catalogs of mollusks until Tubangui (40) established its intermediate host status in his paper on "The Molluscan Intermediate Host in the Philippines of the Oriental Blood Fluke *Schistosoma japonicum* Katsurada."

Following Tubangui, Rensch (41), to whom some of these mollusks were sent for determination, christened them *Oncomelania hydrobiopsis* in 1932.

In 1934 Bequaert (44) published "The Molluscan Intermediate Host of the Blood Fluke, *Schistosoma japonicum* Katsurada", where he calls it *Blanfordia quadrasi*, and makes *Oncomelania hydrobiopsis* Rensch synonymous with it.

#### GENERIC DEFINITION

*Shell*.—Shell small, elongate-ovate, thin, horn-colored or darker, with a slender dark line bordering the peristome. Nuclear whorls 2.0, inflated, strongly rounded, glassy, appearing finely granulated under very high magnification. Postnuclear whorls inflated, well rounded, marked by retractively slanting lines of growth, which in *hydrobiopsis* assume almost the strength of threads. In this they are rather coarse and closely approximated. In the other two species the indication of axial sculpture, although similar, is very much reduced, that is, merely indicated. Suture strongly constricted; periphery inflated, well rounded. Base short, inflated, strongly rounded, narrowly umbilicated. There is a thickening of the outer lip behind the aperture into a callus, which is scarcely indicated in *minima*.

*Operculum*.—Operculum thin, horny, paucispiral, consisting of only 1.5 whorls, which have the nucleus excentric.

*Radula*.—The radula is small and has a rachidian tooth with 5 denticles, of which the middle one is the largest and the other two decrease in size. There are only 2 basals on each side present in this



genus. The formula for it, therefore, is  $\frac{2-1-2}{2-2}$ . The median tooth is oblique, similar in shape to that of the other genera and bears 7 denticles, of which the median is much larger than the rest. The first marginal varies from 8 to 9 in the different species, and the outer marginal from 8 to 6.

*Animal*.—Of this I know nothing, except the features described under shell, operculum, and radula. Of its ecology I may quote from Dr. Tubangui (40):

The Philippine snail further agrees with the other species of *Blanfordia*, or *Oncomelania*, in its amphibious habits. It was very seldom encountered under water, but most frequently under dead leaves and other objects in moist surroundings above the edge of the water. It was also often seen attached to the stems and leaves of grasses and other weeds and to such objects as house and bridge posts, its position in every case being just a few millimeters above the surface of the water. It was never met with in the vicinity of principal rivers or their branches where the current is rapid, but seems to prefer small bodies of water where there is very little, if any, current. It appears to be a dirty feeder, for it was collected in largest numbers along the banks of a small mountain brook, a pond, a terminal irrigation canal, and irrigated rice paddies, where there are houses and where the presence of human faeces was very apparent. \* \* \* the Philippine mollusk can withstand prolonged desiccation, at least up to four weeks under laboratory conditions.

#### SCHISTOSOMOPHORA QUADRASI (Möllendorff)

Plate 1, fig. 8; plate 2, fig. 5; plate 3, fig. 1

1895. *Prososthenia quadrasi* MÖLLENDORFF, Nachrichtsbl. Deutsch. Malakoz. Ges., vol. 27, p. 138.

1932. *Prososthenia quadrasi* TUBANGUI, Philippine Journ. Sci., vol. 49, pp. 298-301.

1932. *Blanfordia quadrasi* TUBANGUI, Philippine Journ. Sci., vol. 49, pp. 298-301, pl. 2, fig. 3.

1934. *Prososthenia quadrasi* BEQUAERT, Journ. Parasit., vol. 20, pp. 280-282.

Shell small, regularly elongate-conic, thin, semitranslucent, horn-colored with the edge of the peristome marked by a line of chestnut brown. The first turn of the nucleus has been lost; the last is rounded, smooth, and, under high magnification, minutely granulose. Post-nuclear whorls very inflated, strongly rounded, and marked by feeble, almost vertical, incremental lines which give one the impression of very fine threads, closely approximated when viewed under high magnification. Indications of spiral striations here are more pronounced than in *Schistosomophora hydrobiopsis*. Suture strongly constricted; periphery inflated, strongly rounded. Base inflated,



strongly rounded, moderately broadly umbilicated, a little more so than in *Schistosomophora hydrobiopsis*. The outer lip is reenforced by a heavy callus a little behind the peristome. Aperture broadly oval and rather broadly expanded and reflected, adnate to the preceding turn at the parietal wall. The operculum is thin, horny, and has 1.5 whorls, which are excentric. In the radula the rachidian tooth has the formula  $\frac{2-1-2}{2-2}$ . The median has 7 denticles, of which the middle one is much larger than the rest. The inner marginal has 8 denticles, the outer 7.

The specimen described and figured, U.S.N.M. no. 420943, a paratype, received from the von Möllendorff Collection, was collected by 'Quadrass at Surigao, Mindanao, Philippine Islands. It has 5.9 whorls, and measures: Height, 5.2 mm; diameter, 3.0 mm.

This species differs from *Schistosomophora hydrobiopsis* in being stouter and having the whorls more inflated, the axial sculpture finer and closer spaced and indications of spiral sculpture stronger, and in having 7 denticles in the outer marginal tooth of the radula.

#### SCHISTOSOMOPHORA HYDROBIOPSIS (Rensch)

Plate 1, fig. 7; plate 2, fig. 6; plate 3, fig. 2

1932. *Oncomelania hydrobiopsis* RENSCH, Philippine Journ. Sci., vol. 49, pp. 551-552, figs. 1a-c.  
 1932. *Blanfordia quadrasi* TUBANGUI, Philippine Journ. Sci., vol. 49, pp. 298-299, pl. 2, fig. 3, pl. 5, fig. 1.  
 1932. *Prososthenia quadrasi* TUBANGUI, Philippine Journ. Sci., vol. 49, pp. 298-299, 301.  
 1934. *Blanfordia quadrasi* BEQUAERT, Journ. Parasit., vol. 20, pp. 280-281.  
 1934. *Oncomelania hydrobiopsis* BEQUAERT, Journ. Parasit., vol. 20, p. 281.  
 1934. *Prososthenia quadrasi* BEQUAERT, Journ. Parasit., vol. 20, pp. 280-281.

Shell small, elongate-ovate, thin, light horn-colored, with the nuclear whorls transparent; a slender chestnut-brown line edges the peristome. Nuclear whorls 2.0, inflated, strongly rounded, glassy, appearing finely granulated under very high magnification. Post-nuclear whorls moderately inflated, strongly rounded, and marked by rather strong, slightly retractively curved lines of growth which almost constitute axial riblets. In addition to this there are faint indications of spiral sculpture—so faint that only under certain angles of the light does this become apparent, chiefly about the periphery and the upper portion of the base. Suture strongly constricted; periphery inflated, well rounded. Base short, moderately umbilicated, marked by the same sculpture as the spire. The outer lip is reenforced

behind the peristome by a very heavy callus which extends down to the base. Aperture broadly ovate, slightly expanded and reflected and adnate to the preceding turn at the parietal wall. The operculum is thin, corneous, and consists of 1.5 whorls. It has an excentric nucleus. In the radula the rachidian tooth has the formula  $\frac{2-1-2}{2-2}$ .

There are 7 denticles on the lateral tooth, of which the middle is by far the heaviest. Both the first and second marginals have each 8 denticles.

U.S.N.M. no. 426101 contains 17 topotypes collected by Dr. Tubangui, and presented to us by Dr. Faustino of the Philippine Bureau of Science, from Polo, Leyte, the type locality. Fifteen of these have yielded the following measurements:

	No. of whorls	Height in mm	Diameter in mm
U.S.N.M. no. 426101.....	6.2 <sup>a</sup>	4.6	2.7
	6.5	4.7	2.6
	5.7	4.9	2.7
	5.5	5.0	2.8
	5.4	4.9	2.9
	5.5	4.7	2.7
	5.7	3.9	2.5
	6.1	4.3	2.5
	6.2	4.3	2.6
	5.8	4.1	2.5
	5.7	3.9	2.4
	4.3	3.7	2.4
	5.6	3.7	2.2
	4.8	4.7	2.8
	5.1	4.7	2.7
Greatest .....	6.5	5.0	2.9
Least .....	4.3	3.7	2.2
Average .....	5.6	4.4	2.6

<sup>a</sup> Figured specimen.

*Schistosomophora hydrobiopsis* can be distinguished from *quadrasi* by the stronger axial sculpture and by the narrow umbilicus and in having 8 denticles in both marginals.

SCHISTOSOMOPHORA MINIMA, n. sp.

Plate 1, fig. 9; plate 2, fig. 7; plate 3, fig. 3

Shell minute, elongate-ovate, thin, horn-colored, with the outer edge marked by a hairline of chestnut brown. Early whorls decollated in all our specimens, those remaining, inflated, strongly rounded and

marked by retractively curved lines of growth, which on the last whorl suggest obsolete threads of irregular width and spacing. In addition to this there are feeble, poorly defined, spiral lirations which are best seen on the last turn. Suture strongly constricted; periphery inflated, strongly rounded. Base short, moderately broadly umbilicated and marked by the same sculpture that characterizes the last whorl. Aperture large, broadly ovate, with the peristome slightly expanded and reflected. The thickening on the outer lip behind the peristome characteristic of the other members of the group almost absent. The operculum is thin, corneous, and consists of 1.5 turns with the nucleus strongly excentric. In the radula the rachidian tooth has 5 denticles, of which the median is the strongest. There are 4 basals, that is, the formula is  $\frac{2-1-2}{2-2}$ . The lateral tooth is very oblique and has 7 denticles, of which the middle one is much stronger than the rest. The inner marginal has 9 denticles and the outer 6.

The type, U.S.N.M. no. 420950, was collected by Mr. Hirase at Noto, Honshu Island, Japan. It has 3.4 whorls remaining, the apical ones of which are badly eroded, and measures: Height, 3.5 mm; diameter, 2.4 mm.

Two additional specimens, U.S.N.M. no. 346039, yields the following measurements: 2.5 and 2.7 whorls; height, 3.4 and 3.0 mm; diameter, 2.2 and 2.3 mm, respectively.

This species is much smaller than the two Philippine members and has a quite different formula for the outer radular tooth.

These shells were sent to us by Y. Hirase under the name *Blanfordia minima* Hirase. I have been unable to find a description of this, and therefore consider that the name is new.

#### ONCOMELANIA Gredler

*Genotype*.—*Oncomelania hupensis* Gredler.

From the very first to the last published paper upon members of this genus doubt and uncertainty seem to have possessed the minds of the students reporting upon them.

Gredler (5), in creating the genus and species *Oncomelania hupensis*, devotes considerable space to the justification of this act. Heude (8), after describing six new species and recognizing two of the previously named forms, also seems to have been puzzled about the many forms which he described, for he says:

In the presence of the forms figured on plate 33, everybody is at liberty to decide for himself whether we have only local modifications of the same thing in different localities which would be nothing but simple varieties, or if those

modifications are sufficient to adopt the specific names here proposed. In the former case we would have nothing but varieties of the earlier *Oncomelania hupensis* Gredler \* \* \* which would mean that the province of Hupeh is the mother country of the prototype. There is nothing against this because from the appearance of this species this territory more than in our days must have been a vast fresh-water sea, mixing the waters of lakes Po-yang and Tong-ting with those of the upper Yangtze.

From that time to Dr. Li's able efforts, doubt and uncertainty as to the scientific status of the named species have obtained.

I hope that definitely separating the Katayamas from the *Oncomelania*s will remove some of the difficulties. Also that the recognizing of Heude's species and the adding of some more will stimulate the collecting and studying of material from many more localities and that this may result in removing the doubts expressed by Heude, which I am not altogether able to allay.

#### HISTORY

This genus was established in 1881 by Vincenz Gredler (5) for *Oncomelania hupensis* Gredler. He based his contention on three specimens collected by P. Fuchs in March at "U-tschang-fu" (Wuchang, Hupeh Province).

The next to add to our knowledge of the group was O. F. von Möllendorff (6), who in 1888 believed that *Oncomelania* Gredler should be replaced by the earlier *Prososthenia* Neumayr, in which we do not concur, but in spite of his contention he here also describes and figures *Oncomelania schmackeri* collected by Schmacker "near Shanghai."

In 1889 R. P. M. Heude (7) discusses *Prososthenia* and *Oncomelania* and states that the latter name is not suitable because it suggests affinities with *Melania*, while in reality the mollusks in question he believes belong to the Rissoidae. He states that for a long time they have had this labeled *Hemibia* in their museum, and he therefore rechristens it *Hemibia* on account of the amphibious habits of the animal. *Hemibia*, therefore, is a pure and simple synonym of *Oncomelania* with the same type, *i. e.*, *Oncomelania hupensis* Gredler.

In 1890 B. Schmacker and O. Böttger (9) discuss *Prososthenia schmackeri* and state that they have typical specimens from the hills near Shanghai; Kah-ding (Kashing) near Shanghai; Chapoo (Chapu) on Hang-choo (Hangchow) Bay and Kiukiang (Kiangsi Province). Here also they describe *Prososthenia moellendorffi* from Ningkuofu (Ningkwofu), Anhwei Province.

By far the most extensive work on the group was done by P. M. Heude (8), who, in the same year, 1890, published six additional species in his memorable work on the terrestrial and freshwater mollusks of the valley of the Fleuve Bleu. Here he refers all the species to the genus *Hemibia*. He gives figures of the shell of *Hemibia schmackeri* on plate 33, figure 1a, and of the soft parts on the same plate in figures 1 to 5, and of the radula, figure 7 (enlarged 400 times). The material upon which these studies are based came from "Grand Lac" (Lake Tai Hu).

He here lists *Hemibia hupensis* Heude, which his figure 19, plate 33, plainly proclaims to be *Oncomelania schmackeri*.

His next species is *Hemibia sublevis*, which he figures on plate 33, figure 15. This figure agrees with Schmacker and Böttger's description and figure of *Oncomelania moellendorffi*, and comes from almost the same locality.

Both *Oncomelania moellendorffi* and *Oncomelania sublevis* were described in 1890. Schmacker and Böttger's paper was published in the July-August number of the *Nachrichtsblatt*. No exact date for Heude's publication is available. It was reviewed in October. I shall accept the name *moellendorffi*, unless it is proved to be antedated by *sublevis*, because it was better described.

His next species, *Hemibia carectorum*, is figured on plate 33, figure 16, and is said to come from the left bank of the Yangtze opposite Nanking; this I believe also to be merely a form of *Oncomelania schmackeri*.

His next species, *Hemibia luteola*, we also feel is nothing but a variant of *Oncomelania schmackeri*; it is his figure 17.

*Hemibia crassa* Heude, plate 33, figure 18, comes from farther up the Yangtze, namely, "Tong-lieou" (Tungliuhs), Anhwei Province. We have no specimens from that region and quote his text and figure.

His next species, *Hemibia longiscata*, is figured on plate 33, figure 20, and comes from opposite "Kin tcheou-fu" (Kingchowfu), Hupeh Province.

His last species, *Hemibia costulata*, like the foregoing, represents the most western location known. He does not figure it, but the sculptural characters and size make me hesitate to refer it to the large species. We shall, therefore, consider it distinct and quote his description. It comes also from the same locality as the last.

Heude's many names and the lack of comparative material evidently held up further advances in our knowledge of *Oncomelania*. It was

not until these mollusks were implicated as intermediate hosts of *Schistosoma japonicum* that a renewed interest was manifested.

Bavay and Dautzenberg (18, p. 38), in their "Description de Coquilles Nouvelles de L'Indo-Chine", discuss *Oncomelania* and *Hemibia*.

In 1923 Meleney and Faust (29) demonstrated that *Oncomelania* served in the Soochow area as intermediate host of *Schistosoma japonicum*.

In 1924 Faust (34) published "Schistosomiasis in China", in which he states that he and Meleney also found what they called *Katayama nosophora*, which I named in 1925 *Katayama fausti*, to be a carrier.

In the same year appeared Faust's (33) paper, "Notes on Larval Flukes from China", in which he cites all the localities in which they have demonstrated intermediate hosts.

Faust here states that:

These forms are all amphibious in habits. They are not found in large or swift bodies of water, but in among the grass and weeds and moist humus of overhanging banks all along terminal canals and quiet coves. They are also found in the rice nursery beds \* \* \* The snails do not live in clayey soil, but can usually be located near freshly deposited human fertilizer. The region north of the Yangtze Valley is incompatible to their existence. Here, too, the *Oncomelania*s are found only in streams with considerable lime supply.

Faust and Meleney's schistosomiasis studies in China resulted in Nelson Annandale's researches in intermediate host subject. His studies (31) are recorded in 1924 in his paper on "The Molluscan Hosts of the Human Blood Fluke in China and Japan, and Species Liable to be Confused with Them", where he expresses the conclusion that *Katayama* of Robson is not generically distinct from *Oncomelania*. He fails to recognize true *Oncomelania hupensis*, citing 8 mm for its height, though that species is almost half again that size. He lumps all of Heude's species under *Oncomelania hupensis*, retaining only as doubtfully specifically distinct, *Oncomelania longiscata* and *Oncomelania sublaevis*. Such a conclusion is not surprising, considering the scant material available for his studies. He establishes two sections: *Katayamae* and *Hemibiae*. In the first he places *Oncomelania nosophora* (Robson) and *Oncomelania formosana* (Pilsbry). His *Hemibiae* embraces *Oncomelania hupensis* Gredler, in which species he includes *Melania* (? *Sulcospira*) *schmackeri* Böttger erroneously, also Heude's *Hemibia schmackeri*, *carectorum*, *luteola*, *crassa*, and *costulata*, and *Oncomelania sublaevis* (not *sublevis* Heude) and *longiscata*. His treatment of *Blanfordia* has been discussed under that genus.



In 1924 Faust (33, p. 276) states of *Katayama* in China that the *Katayama* species appear to live only in mountain stream water, and the *Oncomelania* species have been found only in water with considerable lime supply.

Bartsch (35), in his paper on "Some new Intermediate Hosts of the Asiatic Human Blood Fluke", refers to *Oncomelania*.

In 1926 L. Germain and M. Neveu-Lemaire (36), in their "Essai de Malacologie Medicale", make *Hemibia* Heude, 1889, a subgenus of *Oncomelania* and recognize under this *Oncomelania* (*Hemibia*) *hupensis* Gredler, *Oncomelania* (*Hemibia*) *sublaevis* Heude and *Oncomelania* (*Hemibia*) *longiscata* Heude. They give enlarged figures of a shell which they consider *Oncomelania* (*Hemibia*) *hupensis*, but which in reality is *Oncomelania schmackeri* Möllendorff.

In 1928 Bequaert (37) in his exhaustive paper, "Mollusks of Importance in Human and Veterinary Medicine", refers *Oncomelania hupensis* to *Hemibia*.

Thiele (38), in his "Handbuch der Systematischen Weichtierkunde", 1929, page 150, considers *Hemibia* of Heude and *Katayama* of Robson synonymous with *Oncomelania*.

Tubangui (40), in his paper, 1932, "The Molluscan Intermediate Host in the Philippines of the Oriental Blood Fluke, *Schistosoma japonicum* Katsurada", refers to *Oncomelania*.

Rensch (41), in his "Eine Neue Hydrobiidae von den Philippinen", calls his shell *Oncomelania hydrobiopsis*. I have here rechristened it *Schistosomophora hydrobiopsis*.

Bequaert (44) in his 1934 paper, "The Molluscan Intermediate Host of the Blood Fluke, *Schistosoma japonicum* Katsurada", in the Philippines discusses the relationship of this animal to *Oncomelania*.

By far the most important paper, from a molluscan standpoint, was contributed by Dr. Fu-ching Li (46), "Anatomie, Entwicklungsgeschichte, Oecologie und Rassenbestimmung von *Oncomelania*, des Zwischenwirtes von *Schistosoma japonicum* (Katsurada 1904) in China." He here gives a very careful anatomic and embryologic, as well as ecologic, study of *Oncomelania*. I have quoted extensively from this in my introduction to the genus.

#### GENERIC DEFINITION

*Shell*.—The shell of *Oncomelania* is elongate-conic, moderately thick. It is covered with a yellow, greenish, or olivaceous periostracum, which darkens materially at the edge of the peristome. Nuclear whorls 2, well rounded, smooth except for microscopic granules. The



early postnuclear whorls are marked by incremental lines and gradually developing axial ribs which vary materially in strength and spacing in the various species. These ribs extend over the periphery and base but become enfeebled toward the umbilicus. The spaces between the ribs, as well as the axial ribs themselves, are marked by slender threadlike incremental lines which also vary decidedly in strength. In addition to this, these incremental lines in some of the species are flexed at more or less regular intervals, which tends to give them a spiral sculpture effect. In mature shells a strong varix is present a little behind the edge of the peristome of the outer and basal lip, which in some of its species decidedly thickens even the base of the columella. Suture strongly impressed. Periphery rounded. Base narrowly umbilicated. Aperture somewhat oblique, varying from oval to subquadrate. Peristome thin, expanded and reflected, adnate to the preceding whorl at the parietal wall.

*Operculum*.—The operculum is thin, corneous, paucispiral, having 2.2 whorls, with very excentric nucleus. The operculum in number of whorls therefore agrees with *Blanfordia*, but is much smaller and with more excentric nucleus.

*Radula*.—The radula of the various species of *Oncomelania* show no diversions in the rachidian or lateral teeth. The rachidian tooth has 3 denticles on the free edge, of which the central is the larger. It also has two pairs of basals; its formula, therefore, is  $\frac{1-1-1}{2-2}$ . In this respect it stands between *Katayama*, which has the formula  $\frac{1-1-1}{3-3}$ , and *Schistosomophora*, which has the formula  $\frac{2-1-2}{2-2}$ . The lateral tooth is very oblique and bears 6 denticles, of which the third from the inside is by far the largest. This may be designated as 2-1-3, in which respect it agrees with *Katayama*, but not *Schistosomophora*, which has 3-1-3. It is in the inner marginal that we find considerable variation. One group has 9, a second 7, and another 6 denticles. The outer marginal bears 5 denticles, of which the inner is larger than the rest, in which character it agrees with both *Katayama* and *Schistosomophora*.

*Animal*.—The animal of *Oncomelania schmackeri* was figured by Heude (8), plate 33, figures 1-7. Li (46) also based his splendid anatomic and embryologic studies on this species.

I have not seen living specimens and would have to quote from these sources; I prefer to refer students to Dr. Li's careful and

detailed study. I may merely call attention to the fact that the foot in *Blanfordia* is divided, while that of *Oncomelania* is entire.

*Egg*.—Li (46) states, pages 128-9, that he found the eggs at Djia Schan in 1933 laid in the water in April and May in masses of 15-30 enclosed in a jelly mass and attached to stones and plants. This also distinguishes them from those of *Katayama*, whose eggs are deposited singly or in short chains.

*Ecology*.—Of *Hemibia hupensis*, Faust and Meleney (32) write:

In warm weather it inhabits the moist earth, just above the water's edge, always within 50 cm. of the water and usually within 10 cm. of it. It is found attached to the earth, to stones or to the stems of grass or plants growing out of the water. It prefers sloping banks but avoids exposure to the sun. It must therefore be searched for in secluded spots, beneath loose grass, under projecting clods of earth or beneath stones. The bodies of water on whose shores it is found are relatively clear, cool and still. It has not been found in large canals where there is much traffic and where there is, therefore, much movement of the water, but may be found not over four or five meters from such a canal, in a small terminal branch. It may be found singly or in groups. . . . It is occasionally found on stones or roots of grass, a few centimeters below the surface of the water, but dredgings of deep water-grass have not been found to contain it, nor has it been found in the bottom of a canal on whose shore it was abundant.

In the laboratory, if placed in a deep glass dish in shallow water, it usually climbs out from the water in a few minutes, on the side of the dish away from the window, and, after creeping far enough to free itself from water, will fasten its shell to the glass by mucus at the aperture, retreat into its shell and remain there for hours or days. It may drop or creep back into the water, or may possibly remain desiccated until death. Reimmersion in water after such drying, usually brings the snail rapidly out of its shell and into full activity.

#### KEY TO THE SPECIES OF ONCOMELANIA<sup>4</sup>

Denticles on the marginal teeth 9: 5.

Axial ribs 20 or more per whorl.....*moellendorffi*.

Axial ribs 18 or less per whorl.....*longiscata*.

Denticles on the marginal teeth not 9: 5.

Denticles on the marginal teeth 7: 5.

Axial ribs poorly developed.....*elongata*.

Axial ribs strongly developed.

Incremental lines strong.....*hupensis*.

Incremental lines feeble.....*schmackeri*.

Denticles on the marginals not 7: 5.

Denticles on the marginals 6: 5.....*multicosta*.

<sup>4</sup> Heude's *Hemibia crassa* and *Hemibia costulata* are not included in this key for want of material from the type locality.

Summary of Characters of the Species of *Oncomelania* <sup>a</sup>

Name	Radula formula	No. of whorls remaining	No. of axial ribs per whorl	Height in mm	Diameter in mm
<i>moellendorffi</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 9 : 5$	6.14	22.27	7.35	3.24
<i>longiscata</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 9 : 5$	6.38	12.65	8.04	3.77
<i>elongata</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 7 : 5$	8.95	16.04	9.45	3.80
<i>hupensis</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 7 : 5$	7.02	12.50	8.21	3.76
<i>schmackeri</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 7 : 5$	5.85	15.29	7.41	3.58
<i>multicosta</i>	$\frac{1-1-1}{2-2} : 2-1-3 : 6 : 5$	6.60	21.50	8.05	3.48

<sup>a</sup> *Oncomelania crassa* and *Oncomelania costulata* are not included for lack of material.

## ONCOMELANIA MOELLENDORFFI (Schmacker and Böttger)

Plate 1, fig. 19; plate 2, fig. 18; plate 5, fig. 1

1890. *Prososthenia moellendorffi* SCHMACKER and BÖTTGER, *Nachrichtsbl. Deutsch. Malakoz. Ges.*, vol. 22, pp. 126-7, pl. 2, fig. 7.
1890. *Hemibia sublevis* HEUDE, *Mem. Concern. Hist. Nat. Emp. Chinois*, p. 168, pl. 33, fig. 15.
1924. *Oncomelania sublaevis* ANNANDALE, *Amer. Journ. Hyg., Mon. Ser.* no. 3, p. 287.
1926. *Oncomelania (Hemibia) sublaevis* GERMAIN and NEVEU-LEMAIRE, *Ann. Parasit.*, vol. 4, p. 294.
1932. *Oncomelania moellendorffi* RENSCH, *Philippine Journ. Sci.*, vol. 49, p. 552.

Shell elongate-conic, the early whorls a little paler than the later, which are olive-colored. The postnuclear whorls are moderately rounded and crossed by rather retractorily slanting axial ribs, which are about as wide as the spaces that separate them. Of these ribs 19 occur on the last turn behind the varix, 29 on the penultimate, 31 on the third from the last, 27 on the fourth from the last, 26 on the fifth from the last and 12 on the ribbed portion of the seventh whorl. The parts preceding this are not definitely ribbed. The varix behind the peristome is moderately strong. The intercostal spaces and ribs are marked by rather fine, feebly developed incremental lines. Suture moderately constricted. Periphery well rounded. Base slightly elongated and marked by the continuation of the axial ribs which extend onto the umbilicus. Aperture obliquely oval with the peristome slightly expanded and reflected and edged with a dark line, adnate to the preceding turn at the parietal wall. The operculum is typically oncomelanid. The radula presents the formula  $\frac{1-1-1}{2-2} : 2-1-3 : 9 : 5$ .

The specimen described and figured, U.S.N.M. no. 426221, has 6.4 whorls remaining, and measures: Height 8.1 mm; diameter 3.3 mm. This and 26 additional specimens were collected by Dr. Mary N. Andrews at Cha Hsien, Chekiang Province, China. Ten of these yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7	8
6.1	7.1	3.1	18	18	21	21	22	7+		eroded
6.4	7.6	3.2	+14	23	22	22	4+			"
6.5	7.9	3.3	21	26	28	27	23+			"
6.6	8.2	3.4	19	21	24	24	22			"
6.6	7.4	3.0	19	26	25	24	2+			"
6.2	7.5	3.2	18	20	23	22	24			"
6.4	8.1	3.3	19	29	31	27	26	12+		"
6.0	8.0	3.3	21	21	20	21	22	21+		"
8.4 <sup>a</sup>	7.8	3.2	20	20	22	20	22	20		"
5.1	6.8	3.2	21	27	22	21	15+			"

Ribs per whorl

Greatest .....	21	29	31	27	26
Least .....	14	18	20	20	22
Average .....	19	23.1	23.8	22.9	23.0

<sup>a</sup> Apex entire.

U.S.N.M. no. 428584 contains 19 specimens received from Dr. Y. T. Yao, of the Central Field Health Station, National Government of the Republic of China, collected at Cha-Hsien, Chekiang Province.

Another lot, U.S.N.M. no. 428575, 10 specimens from the same source collected at Pucheng, Nanking, Kiangsu Province.

This species is distinguished from the other that has the marginal teeth radula formula of 9:5 by its much greater number of axial ribs and finer incremental lines.

**ONCOMELANIA LONGISCATA (Heude)**

Plate 1, fig. 20; plate 2, fig. 19; plate 5, fig. 2

1890. *Hemibia longiscata* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 169, pl. 33, fig. 20.

1924. *Oncomelania longiscata* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 287.

1926. *Oncomelania (Hemibia) longiscata* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, p. 294.

Shell rather broadly elongate-conic, stout, horn-colored, with the postnuclear whorls strongly rounded and marked with very heavy

and rather distantly spaced axial ribs, of which 11 occur on the last whorl behind the varix, 14 on the penultimate, 11 on the third and fourth from the last, 12 on the fifth from the last, and 15 on the sixth from the last whorl. The intercostal spaces, as well as the ribs, are marked by strong incremental lines which have a decided wavy aspect. Suture strongly constricted. Periphery well rounded. Base slightly elongate, well rounded, narrowly umbilicated and marked by the continuation of the axial ribs and incremental lines which extend into the umbilicus. There is a strong varix a little distance behind the peristome. Aperture broadly oval; peristome thickened and reflected and adnate to the preceding turn at the parietal wall. The operculum is typically oncomelanid. The radula presents the formula  $\frac{1-1-1}{2-2} : 2-1-3 : 9 : 5$ .

The specimen described and figured, U.S.N.M. no. 420953, as well as the other specimens entered under this catalog number, were collected by Dr. H. E. Meleney on the shore of Lake Tung Ting, near the city of Yochow, Hunan Province, China. Ten specimens from this lot yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7
7.4 <sup>a</sup>	9.2	3.7	11	14	11	11	12	15	eroded
6.6	8.2	3.8	16	15	14	12	15		"
6.6	8.2	3.9	13	14	14	13	15	5+	"
6.4	9.0	4.0	12	14	13	12	13	15	"
6.7	9.3	4.1	12	14	12	12	12	16	"
6.3	9.2	4.2	12	13	13	11	11		"
6.5	8.6	4.0	14	14	12	12	11		"
6.3	9.1	4.0	12	12	12	11	12	9+	"
6.1	7.8	3.7	12	13	11	11	11	11+	"
6.4	8.5	3.9	12	12	11	10	12	14	"

Ribs per whorl

Greatest	.....	16	15	14	13	15
Least	.....	11	12	11	10	11
Average	.....	12.6	13.5	12.3	11.5	12.4

<sup>a</sup> Figured specimen.

I believe that it will prove of interest to give the number of whorls and the measurements of the height and diameter of the entire lot of 37 additional specimens, so I am subjoining them here:

No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
6.4	8.1	3.9	5.4	7.6	3.9
6.3	7.8	3.7	5.4	6.7	3.5
7.0	8.3	3.6	5.4	7.9	4.2
6.5	8.3	3.8	5.2	7.3	3.7
6.2	8.1	3.9	7.2	7.5	3.5
6.7	7.9	3.5	7.2	8.0	3.6
6.7	7.6	3.7	6.0	7.2	3.5
6.9	8.7	3.9	6.7	7.9	3.7
7.0	8.4	3.5	6.4	8.6	3.9
6.2	8.2	3.8	6.4	7.3	3.5
6.6	8.1	3.9	6.3	7.7	3.9
6.3	8.1	3.7	6.4	7.9	3.8
7.2	7.3	3.6	6.3	7.4	3.6
6.6	8.6	3.8	5.2	7.1	3.8
7.4	8.9	3.9	6.0	8.1	3.7
5.8	7.6	3.8	6.4	7.8	3.5
6.2	7.7	3.6	5.5	7.7	3.9
7.0	8.1	3.6	6.5	7.7	3.9
5.5	7.6	3.8			
Greatest <sup>a</sup>	.....		7.4	9.3	4.2
Least <sup>a</sup>	.....		5.2	6.7	3.5
Average <sup>a</sup>	.....		6.38	8.04	3.77

<sup>a</sup> Of 47 specimens.**ONCOMELANIA ELONGATA, n. sp.**

Plate 1, fig. 15; plate 2, fig. 15; plate 5, fig. 4

Shell elongate-conic, wax yellow, the remaining nuclear whorls finely microscopically granose. Early postnuclear whorls marked by incremental lines which slowly develop into axial ribs, which are not heavy, rather flattened, of irregular strength and spacing. The intercostal spaces and axial ribs are marked by incremental lines and show a somewhat malleated aspect. Suture strongly constricted. Periphery well rounded. Base well rounded, narrowly umbilicated and marked by the continuation of the axial ribs. There is a very strong varix a little behind the peristome. The aperture is broadly oval with the peristome expanded and reflected and adnate to the preceding turn on the parietal wall. The operculum is typically oncomelanid. The radula has the typical rachidian tooth  $\frac{1-1-1}{2-2}$ , also the typical lateral of 2-1-3; the inner marginal has 7 denticles, the outer 5.

The type, U.S.N.M. no. 420954, was collected by Dr. Li in Chekiang Province. It has 9.5 whorls and measures: Height 10 mm; diameter 4 mm. It has 13 ribs behind the varix on the first whorl, 16 on the



penultimate, 14 on the third from the last, 15 on the fourth from the last, 17 on the fifth from the last, and 15 on the sixth from the last, which is also the last whorl to show developed ribs.

There are three additional specimens, U.S.N.M. no. 420955, which yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6
8.9	9.1	3.7	15	17	15	14	15	11+
9.2	9.8	3.7	15	18	18	17	18	17
8.2 <sup>a</sup>	8.9	3.8	15	17	18	17	16	17

<sup>a</sup> Broken.

This species can be differentiated from the other two that have 7:5 denticles on the marginals by having the shell much more elongate and more whorls, and the ribs much less strongly developed.

#### ONCOMELANIA HUPENSIS Gredler

Plate 1, fig. 17; plate 2, fig. 14; plate 5, fig. 5

1881. *Oncomelania hupensis* GREGLER, Jahrb. Deutsch. Malakoz. Ges., vol. 8, pp. 120-1, pl. 6, fig. 5.
1888. *Prososthenia hupensis* MÖLLENDORFF, Malakoz. Blätt., n. s., vol. 10, pp. 142-3.
1888. *Oncomelania hupensis* MÖLLENDORFF, Malakoz. Blätt., n. s., vol. 10, pp. 142-3.
1890. *Prososthenia hupensis* SCHMACKER and BÖTTGER, Nachrichtsbl. Deutsch. Malakoz. Ges., vol. 22, pp. 126-7.
1890. *Oncomelania hupensis* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 167.
1890. *Oncomelania hupensis* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 170.
1890. *Hemibia hupensis* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 170.
1912. *Oncomelania hupensis* BAVAY and DAUTZENBERG, Journ. Conchyl., vol. 60, p. 38.
1924. *Oncomelania hupensis* FAUST, Amer. Journ. Hyg., vol. 4, p. 275.
1924. *Oncomelania hupensis* FAUST and MELENEY, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 82.
1924. *Oncomelania hupensis* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, pp. 285-7, in part.
1926. *Oncomelania (Hemibia) hupensis* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, p. 294.
1928. *Hemibia hupensis* BEQUAERT, Journ. Trop. Med., vol. 8, p. 177; 224-5.
1929. *Oncomelania hupensis* THIELE, Handb. Syst. Weicht., pt. 1, p. 150.
1934. *Oncomelania hupensis* BEQUAERT, Journ. Parasit., vol. 20, pp. 281-2.

Shell broadly elongate-conic, wax yellow. Nuclear whorls 2, well rounded, minute, granulose, the early succeeding postnuclear turns



marked by incremental lines which gradually develop into ribs on the later whorls. Postnuclear whorls inflated, strongly rounded, marked by very strong, slightly retractorily slanting, axial ribs, of which, in the specimen figured, there are 12 on the last whorl behind the varix, 13 on the penultimate, 12 on the next 3 whorls, 14 on the sixth from the last, and 8 plus on the seventh from the last whorl. The broad intercostal spaces and the ribs are marked by heavy wavy incremental lines. It is the regularity of these waves that suggests spiral sculpture. Suture strongly constricted. Periphery strongly rounded. Base narrowly umbilicated, marked by the continuation of the axial ribs and incremental lines which extend onto the umbilicus. There is a heavy varix behind the peristome on the outer lip. The aperture is broadly ovate. Peristome is thickened and reflected, dark-edged, adnate to the preceding turn at the parietal wall. The operculum is typically oncomelanid. The radula has the formula  $\frac{1-1-1}{2-2} : 2-1-3 : 7 : 5$ .

The specimen described and figured, U.S.N.M. no. 420956, was collected by Dr. H. E. Meleney from ponds just north of the Yangtze River, a few miles east of Hankow, Hupeh Province, China. It has 7 whorls remaining, and measures: Height 9.9 mm; diameter 4.1 mm.

Ten specimens from this lot yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7	8	Apex
6.6	8.8	3.8	12	14	13	14	14	17	smooth		eroded
7.4	9.8	3.9	12	14	13	12	13	17	8+	"	"
7.4	9.4	4.2	11	11	10	9	9	13	5+	"	"
7.8	9.2	4.0	12	15	12	12	12	15	3+	"	"
7.2	9.8	4.2	11	12	14	12	12	13	18	"	"
7.0 <sup>a</sup>	9.9	4.1	12	13	12	12	12	14	8+	"	"
6.7	7.8	3.6	12	13	13	11	14	11+		"	"
7.0	9.0	3.9	14	14	13	13	12	12		"	"
6.5	8.4	3.7	11	13	12	12	11	8+		"	"
6.4	7.9	3.7	13	15	14	14	15				

Ribs per whorl

Greatest . . . .	14	15	14	14	15	17	18
Least . . . . .	11	11	10	9	9	12	
Average . . . .	12	13.4	12.6	12.1	12.4	14.4	

<sup>a</sup> Figured specimen.

Forty additional specimens from the same locality give the following measurements:

No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
7.0	9.3	4.0	6.1	7.7	3.7
7.2	8.4	3.6	5.1	6.8	3.8
6.9	8.5	3.8	6.5	8.0	3.7
7.3	9.3	4.0	6.2	8.5	3.8
6.4	8.6	3.9	7.3	8.4	4.0
7.1	9.1	4.0	6.5	7.8	3.5
6.3	8.3	3.8	8.2 <sup>a</sup>	8.2	3.6
6.5	8.1	3.9	6.6	7.8	3.7
7.2	8.2	3.9	7.3	8.0	3.5
7.2	8.3	3.9	6.2	7.2	3.7
6.4	7.8	3.8	4.9	6.8	3.7
6.6	8.0	3.8	6.4	8.3	3.7
7.0	7.7	3.5	7.2	8.8	4.1
6.8	7.4	3.5	7.2	7.8	3.7
7.7	8.6	3.7	7.3	8.3	3.5
6.7	7.0	3.6	6.5	7.6	3.6
6.6	7.9	3.9	6.8	8.2	3.8
7.4	8.6	3.8	4.7	6.9	3.5
6.9	8.3	3.8	6.6	7.7	3.5
6.3	8.2	3.7	6.4	7.2	3.4
Greatest .....			8.2	9.9	4.2
Least .....			4.7	6.8	3.4
Average .....			6.75	8.23	3.77

<sup>a</sup> Apex entire.

U.S.N.M. no. 428586 contains three specimens received from Dr. Y. T. Yao, of the Central Field Health Station, National Government of the Republic of China, collected at Huangzhou, Anhwei Province.

This species is differentiated from the other two having the marginal denticles 7:5, by having the ribs exceedingly strong and the incremental lines very heavy.

#### ONCOMELANIA SCHMACKERI Möllendorff

Plate 1, fig. 18; plate 2, fig. 17; plate 5, fig. 3; plate 6, figs. 1, 5, 8, 9

1888. *Oncomelania schmackeri* MÖLLENDORFF, Malakoz. Blätt., n. s., vol. 10, p. 143, pl. 4, figs. 4a, b.

1890. *Hemibia schmackeri* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 168, pl. 33, figs. 1-7.

1890. *Hemibia hupensis* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 168, pl. 33, fig. 19.

1890. *Hemibia caretorum* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 169, pl. 33, fig. 16.

1890. *Hemibia luteola* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 169, pl. 33, fig. 17.
1890. *Prososthenia schmackeri* SCHMACKER and BÖTTGER, Nachrichtsbl. Deutsch. Malakoz. Ges., vol. 22, pp. 126-7.
1923. *Oncomelania hupensis* MELENEY and FAUST, Proc. Soc. Exp. Biol. and Med., vol. 20, pp. 216-8.
1924. *Oncomelania hupensis* FAUST, Amer. Journ. Hyg., vol. 4, pp. 269, 274.
1924. *Hemibia hupensis* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3 p. 285, in part, pl. 36, figs. 9-11.
1926. *Oncomelania (Hemibia) hupensis* GERMAIN and NEVEU-LEMAIRE, Ann. Parasit., vol. 4, pp. 294-5, figured.
1929. *Oncomelania hupensis* FAUST, Human Helminthology, p. 136, fig. 47b.
1934. *Oncomelania hupensis* LI, Trans. Sci. Soc. China, vol. 8, pp. 103-45, 36 figs., 2 tables, 2 maps, in part.

Shell broadly elongate-conic, horn-colored, nuclear whorls 2, well rounded, smooth except for microscopic granules. The early post-nuclear whorls are marked by incremental lines which slowly concentrate into ribs. The later postnuclear whorls well rounded, marked by strong, slightly retractively curved axial ribs which are not strongly elevated. In the specimen described and figured, of these ribs 15 occur on the last whorl behind the varix, 17 on the penultimate, 18 on the third from the last, 15 on the fourth from the last whorl, which is the last ribbed whorl. The intercostal spaces and the ribs are marked by slender incremental lines. Suture strongly constricted. Periphery of last whorl well rounded. Base well rounded, narrowly umbilicated, marked by the continuation of the axial ribs and incremental lines which extend into the umbilicus. There is an exceedingly heavy varix a little distance behind the peristome on the outer lip. The aperture is broadly ovate, somewhat expanded and reflected, dark edged and adnate to the preceding turn at the parietal wall. The operculum is typically oncomelanid. The radula has the formula

$$\frac{1-1-1}{2-2} : 2-1-3 : 7 : 5.$$

The specimen described and figured, U.S.N.M. no. 426224, has 7.3 whorls remaining and measures: Height 8.5 mm; diameter 4.0 mm. This lot contains 44 specimens collected by Dr. Mary N. Andrews at Soochow, Kiangsu Province, China. Ten of these, including the specimen described and figured, yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7
5.9	8.1	3.9	14	17	16	16		smooth	eroded
5.1	8.5	3.8	11	14	12	12		"	"
6.2	7.1	3.4	13	13	13	9+		"	"
4.3	6.9	3.9	11	13	15			"	"
7.3 <sup>a</sup>	8.5	4.0	15	17	18	15		"	"
6.3	7.8	3.7	18	17	15	18		"	"
6.5	7.9	3.8	15	17	16	15		"	"
6.0	8.1	3.6	15	14	15	14		"	"
5.5	7.8	3.8	12	16	16	14		"	"
4.5	6.3	3.4	17	19	16	7+		"	"

Ribs per whorl				
Greatest	.....	18	19	18
Least	.....	11	13	12
Average	.....	14.1	15.7	15.2
				14.86

<sup>a</sup> Figured specimen.

To these, 10 additional measurements from the same lot may be added, as follows:

No. of whorls	Height in mm	Diameter in mm
7.7	8.7	3.6
6.9	7.7	3.6
5.0	8.3	4.1
4.4	7.4	3.7
4.5	6.5	3.3
5.0	6.4	3.3
3.2	6.4	3.8
4.2	6.1	3.6
5.0	6.7	3.4
5.3	6.5	3.3
Greatest <sup>a</sup> ..	7.7	8.7
Least <sup>a</sup> .....	3.2	6.1
Average <sup>a</sup> ..	5.44	7.38
		3.65

<sup>a</sup> Of the 20 specimens.

This sending is the nearest to the type locality of *Oncomelania schmackeri*, which von Möllendorff says was established by Schmacker in the environs of Shanghai.

We have a number of other lots from adjacent territory which yield interesting tabular measurements.

U.S.N.M. no. 426226 contains 33 specimens collected by Dr. Mary N. Andrews at Henli (Hsin Yang-Kang), Chekiang Province, China. Ten of these yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7	Apex
7.3	8.4	3.9	13	14	14	14	10+	smooth		eroded
8.4	8.0	3.6	14	16	15	17	15+	"		entire
7.2	8.2	3.5	14	19	17	15		"		eroded
5.6	6.8	3.3	15	15	14	9+		"		"
7.3	7.5	3.6	16	17	16	18		"		"
5.2	7.1	3.4	14	19	18	18	11+	"		"
5.8	6.2	3.0	16	18	17	14+		"		"
6.2	6.4	3.0	14	15	16	19		"		"
5.4	6.0	3.0	16	15	18	12+		"		"
6.2	6.2	3.1	16	17	17	8+		"		"

Ribs per whorl

Greatest	.....	16	19	18	19
Least	.....	13	14	14	14
Average	.....	14.8	16.5	16.2	16.8

	No. of whorls	Height in mm	Diameter in mm
Greatest	.....	8.4	8.4
Least	.....	5.2	6.0
Average	.....	6.46	7.08
			3.34

U.S.N.M. no. 426227 contains 54 specimens collected by Dr. Mary N. Andrews at Kashing, Chekiang Province, China, 10 of which yield the following rib counts and 40 the following additional measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6
5.4	7.7	3.5	14	17	16	15	15	smooth
7.0	7.6	3.6	14	15	14	14		"
6.1	7.4	3.6	16	19	17	15		"
5.2	7.1	3.4	15	15	14	14		"
6.8	9.4	4.0	13	15	17	16	10+	"
6.3	8.1	3.9	14	16	14	16		"
5.9	7.7	3.6	13	14	13	14		"
5.2	7.5	4.0	14	16	18	15		"
6.4	7.5	3.5	16	19	17	16	16	"
6.7	7.5	3.5	15	16	16	16		"

Ribs per whorl.

Greatest	.....	16	19	18	16
Least	.....	13	14	13	14
Average	.....	14.4	16.2	15.6	15.1

No. of whorls	Height in mm	Diameter in mm	No. of whorls	Height in mm	Diameter in mm
5.5	7.3	3.4	5.4	7.2	3.7
5.0	6.7	3.5	5.4	7.5	3.5
6.6	8.2	4.0	4.7	6.8	3.4
5.5	7.4	3.8	5.9	7.1	3.5
5.0	7.2	3.7	4.8	7.1	3.6
7.2	8.6	3.7	5.3	7.0	3.4
6.6	8.0	3.9	6.3	7.5	3.4
6.3	7.4	3.6	4.5	6.9	3.6
7.2	7.6	3.4	4.4	7.3	3.5
6.2	7.8	3.6	5.0	7.0	3.6
5.8	7.7	3.8	4.2	8.5	4.5
7.1	8.9	3.7	5.5	7.5	3.6
5.8	6.8	3.3	5.1	6.6	3.4
6.4	7.8	3.6	5.3	7.1	3.5
6.3	7.2	3.3	5.3	6.4	3.2

Greatest <sup>a</sup> .....	7.2	9.4	4.5
Least <sup>a</sup> .....	4.2	6.4	3.2
Average <sup>a</sup> .....	5.76	7.49	3.61

<sup>a</sup> For the 40 specimens.

U.S.N.M. no. 426225 contains 39 specimens collected by Dr Mary N. Andrews at Chinking, Kiangsu Province, China, which is the type locality of *Oncomelania luteola* Heude, which I consider synonymous with *Oncomelania schmackeri*, 10 of which give the following rib count and 20 the additional measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7
5.7	7.9	3.8	13	15	13	14		eroded	
6.7	8.0	3.8	11	13	12	13		"	
5.0	8.0	4.2	11	14	13	13		"	
6.2	7.8	3.5	13	13	15	14		"	
6.3	7.2	3.5	12	15	16	15		"	
6.7	7.4	3.7	15	17	17	17		"	
4.8	7.8	4.2	12	14	14	15		"	
5.6	7.0	3.6	12	14	15	14		"	
5.4	7.5	3.6	12	15	14	14	15	"	
6.9	8.4	3.9	11	15	16	14		"	

Ribs per whorl

Greatest .....	15	17	17	17
Least .....	11	13	12	13
Average .....	12.2	14.5	14.5	14.3

	No. of whorls	Height in mm	Diameter in mm
	5.6	7.8	3.7
	6.1	8.6	3.6
	4.7	6.8	3.6
	4.5	6.9	3.8
	4.6	6.6	3.5
	4.9	7.0	3.5
	5.6	7.5	3.6
	4.6	6.4	3.5
	4.8	7.0	3.7
	6.2	8.7	3.8
Greatest <sup>a</sup> ..	6.9	8.7	4.2
Least <sup>a</sup> .....	4.5	6.4	3.5
Average <sup>a</sup> ..	5.54	7.51	3.7

<sup>a</sup> For the 20 specimens.

U.S.N.M. no. 428582, 10 specimens received from Dr. Y. T. Yao, of the central Field Health Station, National Government of the Republic of China, collected at Sunkiang, Chekiang Province.

U.S.N.M. no. 428580, 12 specimens received from the same source, collected at Soochow, Kiangsu Province.

U.S.N.M. no. 428577, 5 specimens from the same source, collected at Wukiang, Kiangsu Province.

U.S.N.M. no. 428581, 1 specimen from Kashing, Chekiang Province.

U.S.N.M. no. 428579, 7 specimens from Nanking, Kiangsu Province.

This species can be differentiated from the other two in which the marginal teeth have 7 : 5 denticles, respectively, by being more broadly conic and in having the ribs less strongly developed than *Oncomelania hupensis* and more strongly developed than in *Ocomelania elongata*.

#### ONCOMELANIA MULTICOSTA, n. sp.

Plate 1, fig. 16; plate 2, fig. 16; plate 5, fig. 6

Shell elongate-conic, pale wax yellow, nuclear whorls decollated. Early postnuclear whorls marked by slender incremental lines which gradually develop into ribs. The later whorls well rounded, marked by very regular, rather closely spaced slightly retractorily slanting, axial ribs, of which 21 are present on the last whorl behind the varix, 24 on the penultimate, 21 on the third from the last, 24 on the fourth and fifth from the last and 10 on the sixth from the last, beyond which they are lost. The spaces separating the ribs are about equal to them; spaces and ribs are marked by fine incremental lines. Suture



strongly constricted. Periphery well rounded. Base narrowly umbilicated, marked by the continuation of the axial ribs and incremental lines, which extend into the umbilicus. There is a heavy varix behind the peristome on the outer lip. Periphery broadly ovate, dark edged, expanded and reflected and adnate to the preceding turn at the parietal wall. The operculum is typically oncomelanid. The radula has the formula  $\frac{1-1-1}{2-2} : 2-1-3 : 6 : 5$ .

The type, U.S.N.M. no. 420962, was collected by Dr. Fu-ching Li at Wu Hsing, Chekiang Province, China. It has 6.6 whorls remaining, and measures: Height 8.8 mm; diameter 3.7 mm.

Three additional specimens, U.S.N.M. no. 420963, yield the following measurements:

No. of whorls	Height in mm	Diameter in mm	Ultimate	Penultimate	Antepenultimate	4	5	6	7	8
7.4	8.4	3.4	21	22	19	20	19	6+	smooth	eroded
6.2	7.5	3.4	20	22	19	21	22		"	"
6.2	7.5	3.4	19	22	20	23	27	18+	"	"

U.S.N.M. no. 428585, six specimens received from Dr. Y. T. Yao, of the Central Field Health Station, National Government of the republic of China, collected at Hangchow, Chekiang Province.

This species is readily distinguished from the other *Oncomelania*s by its lesser number of denticles on the inner marginal and by having the ribs much more regularly developed and spaced.

ONCOMELANIA COSTULATA (Heude)

1890. *Hemibia costulata* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, pp. 169-70.  
1924. *Oncomelania hupensis* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 285, in part.

We have not seen specimens referable to this species and give a free translation of Heude's description. He states that figures of it were accidentally omitted from his plate.

It agrees with *Oncomelania crassa* Heude in height and is distinguished from all the other species by the more slender and more numerous axial ribs, which is especially true of the last whorl. The spire is elongate, pointed straight and almost entire.

It was found in company with *Oncomelania longiscata* in the upper mouth of Lake T'ong-t'ing, opposite the village of Kin-tcheoufou.

**ONCOMELANIA CRASSA (Heude)**

Plate 6, fig. 6

1890. *Hemibia crassa* HEUDE, Mem. Concern. Hist. Nat. Emp. Chinois, p. 169, fig. 18.

1924. *Oncomelania hupensis* ANNANDALE, Amer. Journ. Hyg., Mon. Ser. no. 3, p. 285, in part.

The collection of the United States National Museum contains no specimens referable to the species described under this name, nor do we have any specimens from a nearby locality which might be referred to it. I therefore give a free translation of Heude's description and republish his figure.

This species is readily distinguished by its elongate form and the obtuse spire which is rarely entire. The intercostal spaces are wide and distinctly marked by incremental lines, which are also present on the axial ribs. The specimen figured shows that the peristome extends beyond the varix. The edge of the peristome is black, and the periostracum is greenish black. He states that he found this species in winter, a long time out of water, along the edges of the drainage ditches which empty into Lake Tong-lieou in summer.

## REMEDIAL MEASURES

It appears that where the *Katayama*, the *Oncomelania*, and the *Schistosomophora* groups are present, an acid condition of the soil exists. The use of crushed limestone over such territory will change that condition into an alkaline reaction and make it an inhospitable habitat for these mollusks, resulting in their elimination. The absence of a suitable host in a habitat will eliminate the possibility of the worm developing in that region.

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## EXPLANATION OF PLATES

## PLATE I, SHELLS

- FIG. 1. *Katayama nosophora yoshidai* Bartsch, type.  
 2. " *fausti* Bartsch, type.  
 3. " *cantoni* Bartsch, type.  
 4. " *nosophora* Robson.  
 5. " *lii* Bartsch, type.  
 6. " *formosana* Pilsbry and Hirase.  
 7. *Schistosomophora hydrobiopsis* Rensch.  
 8. " *quadras* Möllendorff.  
 9. " *minima* Bartsch.  
 10. *Blanfordia simplex* Pilsbry.  
 11. " *japonica* A. Adams.  
 12. " *integra* Pilsbry, type.  
 13. " *bensoni* A. Adams.  
 14. " *japonica* A. Adams, type.  
 15. *Oncomelania elongata* Bartsch, type.  
 16. " *multicosta* Bartsch, type.  
 17. " *hupensis* Gredler.  
 18. " *schmackeri* Möllendorff.  
 19. " *moellendorffi* Schmacker and Böttger.  
 20. " *longiscata* Heude.

## PLATE 2, OPERCULA

- FIG. 1. *Blanfordia japonica* A. Adams.  
 2. " *integra* Pilsbry.  
 3. " *bensoni* A. Adams.  
 4. " *simplex* Pilsbry.  
 5. *Schistosomophora quadras* Möllendorff.  
 6. " *hydrobiopsis* Rensch.  
 7. " *minima* Bartsch.  
 8. *Katayama nosophora* Robson.  
 9. " *yoshidai* Bartsch.  
 10. " *fausti* Bartsch.  
 11. " *lii* Bartsch.  
 12. " *formosana* Pilsbry and Hirase.  
 13. " *cantoni* Bartsch.  
 14. *Oncomelania hupensis* Gredler.  
 15. " *elongata* Bartsch.  
 16. " *multicosta* Bartsch.  
 17. " *schmackeri* Möllendorff.  
 18. " *moellendorffi* Schmacker and Böttger.  
 19. " *longiscata* Heude.

PLATE 3, RADULAE

- FIG. 1. *Schistosomophora quadras* Möllendorff.  
 2. " *hydrobiopsis* Rensch.  
 3. " *minima* Bartsch.  
 4. *Blanfordia integra* Pilsbry.  
 5. " *japonica* A. Adams.  
 6. " *simplex* Pilsbry.  
 7. " *bensoni* A. Adams.

PLATE 4, RADULAE

- FIG. 1. *Katayama nosophora* Robson.  
 2. " " *yoshidai* Bartsch.  
 3. " *formosana* Pilsbry and Hirase.  
 4. " *lii* Bartsch.  
 5. " *fausti* Bartsch.  
 6. " *cantoni* Bartsch.

PLATE 5, RADULAE

- FIG. 1. *Oncomelania moellendorffi* Schmacker and Böttger.  
 2. " *longiscata* Heude.  
 3. " *schmackeri* Möllendorff.  
 4. " *elongata* Bartsch.  
 5. " *hupensis* Gredler.  
 6. " *multicosta* Bartsch.

PLATE 6

- FIG. 1. Egg mass of *Oncomelania schmackeri* Möllendorff. Copy of Dr. Li's figure.  
 2. Animal of *Blanfordia japonica*. Copy of A. Adams' figure.  
 3. Animal of *Blanfordia bensoni*. Copy of A. Adams' figure.  
 4. Egg chain of *Katayama lii* Bartsch. Manuscript figure by Dr. Li.  
 5. Radula of *Oncomelania schmackeri* Möllendorff. Copy of Heude's figure.  
 6. *Oncomelania crassa*. Copy of Heude's figure.  
 7. *Katayama lii* Bartsch. Single eggs. Manuscript figure by Dr. Li.  
 8. *Oncomelania schmackeri* Möllendorff. Foot. Copy of Dr. Li's figure.  
 9. *Oncomelania schmackeri* Möllendorff. Head. Copy of Dr. Li's figure.

PLATE 7

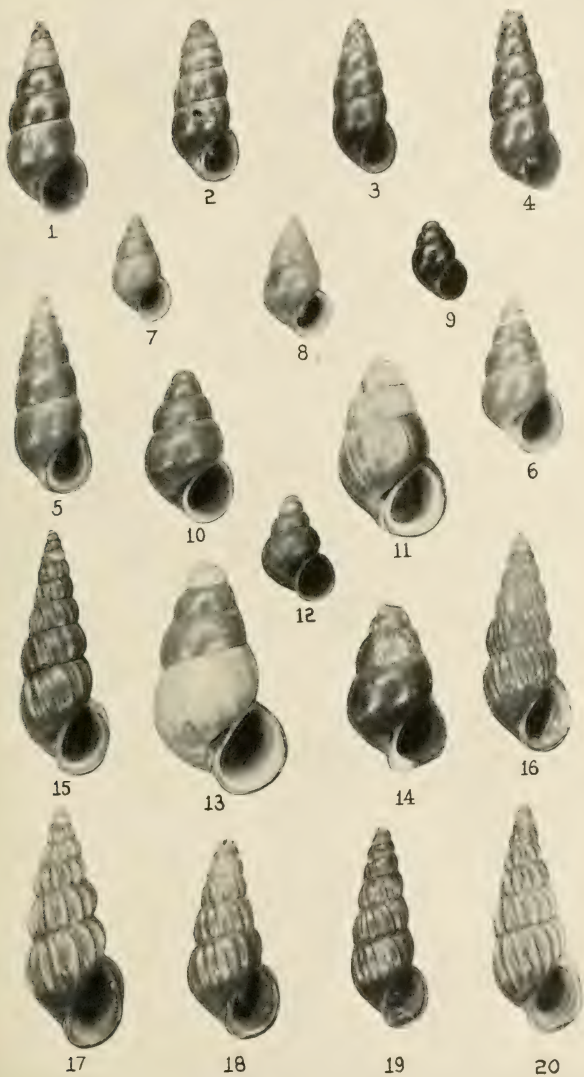
Outline map showing the type localities from which the species of *Blanfordia*, *Katayama*, and *Schistosomophora* were described.



## PLATE 8

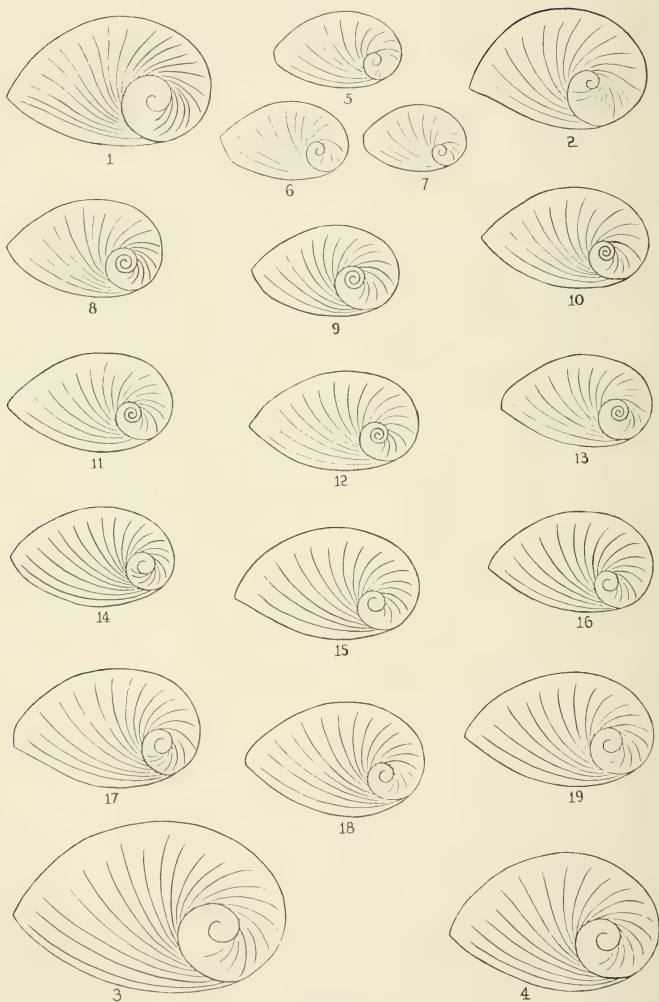
Copy of a topographic map of eastern China, showing the type localities of the described species of *Oncomelania*, as follows:

1. *Oncomelania moellendorffi*
2.       "       *longiscata*
3.       "       *elongata*
4.       "       *hupensis*
5.       "       *schmackeri*
6.       "       *multicosta*
7.       "       *costulata*
8.       "       *crassa*



SHELLS

(For explanation, see page 58.)



OPERCULA

(For explanation, see page 58.)



**RADULAE**

(For explanation, see page 59.)



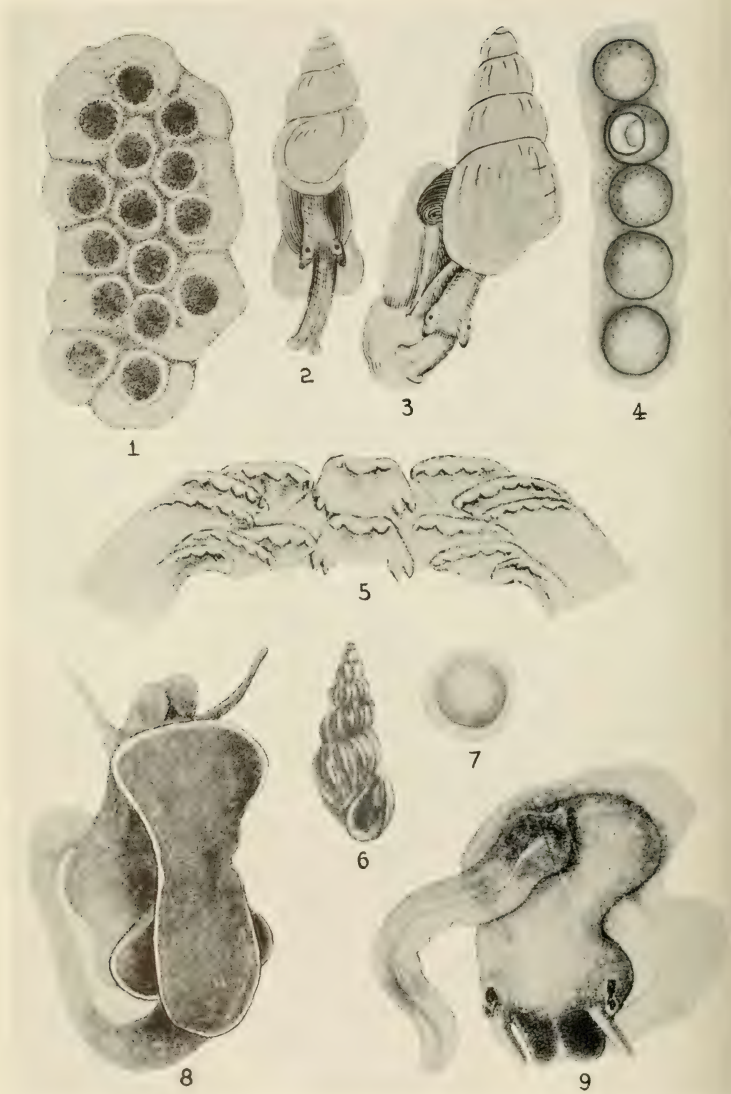
RADULAE

(For explanation, see page 59.)



**RADULAE**

(For explanation, see page 59.)



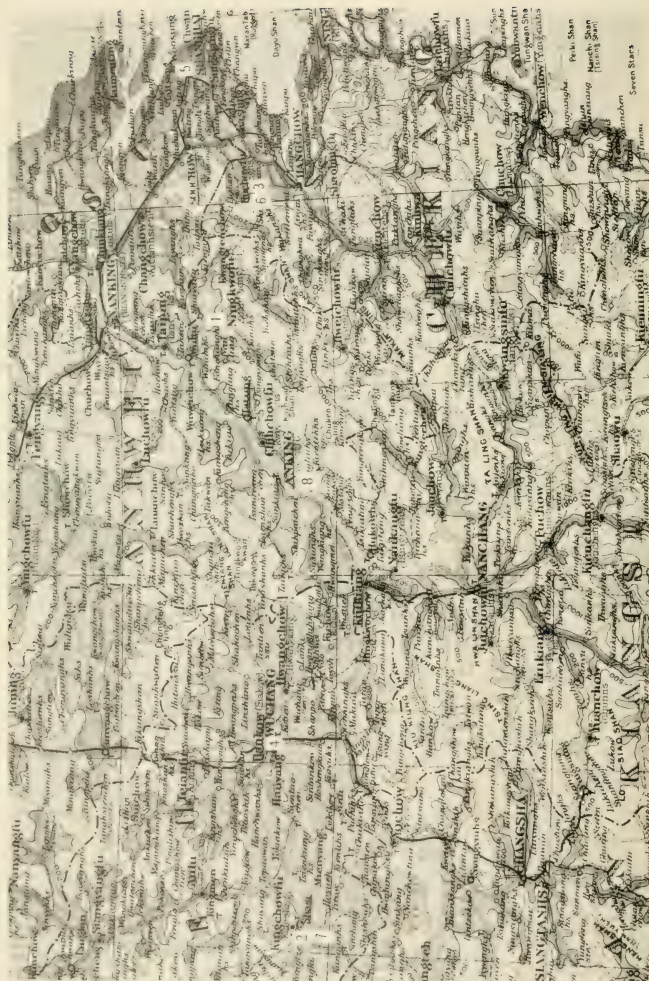
ANIMAL AND EGGS  
(For explanation, see page 59.)





TYPE LOCALITIES OF BLANFORDIA, KATAYAMA, AND SCHISTOSOMOPHORA

(For explanation, see page 59.)



TYPE LOCALITIES OF ONCOMELANIA

(For explanation, see page 60.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 6

# NEW SPECIES OF AMERICAN EDRIOASTEROIDEA

(WITH SEVEN PLATES)

BY

R. S. BASSLER

Head Curator, Department of Geology,  
U. S. National Museum

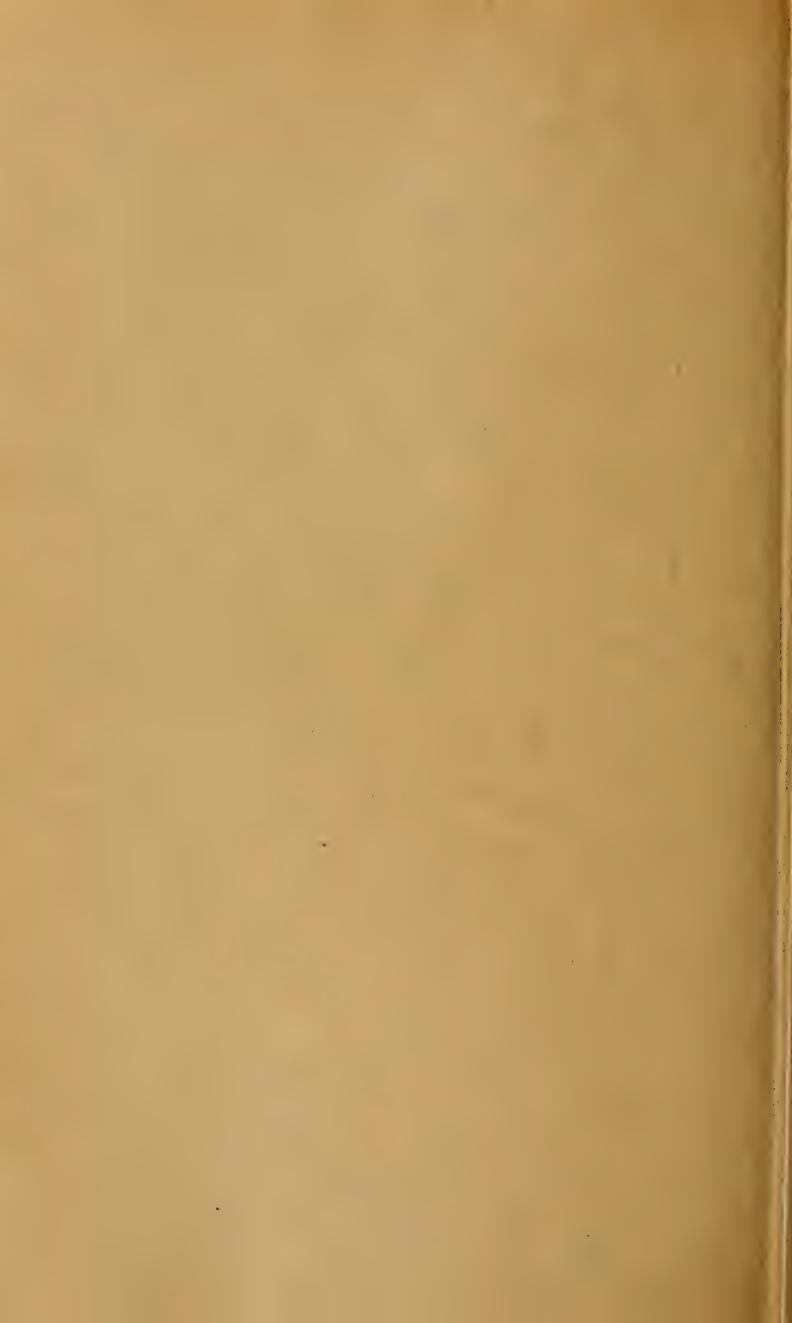


(PUBLICATION 3385)

CITY OF WASHINGTON

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## NEW SPECIES OF AMERICAN EDRIOASTEROIDEA

By R. S. BASSLER

*Head Curator, Department of Geology, U. S. National Museum*

(WITH SEVEN PLATES)

In a recent paper entitled "The Classification of the Edrioasteroidea,"<sup>1</sup> the writer presented a revised classification of this division of primitive Paleozoic echinoderms belonging to or closely related to the cystids. Six new genera were defined, two of which were based on new species, and it was stated that descriptions of additional new species upon which the classification was in part based were in contemplation. The present paper includes these descriptions, as well as comments on and illustrations of previously described species. Its main purpose is taxonomic, and these two articles present to the student a brief résumé of all genera and most of the species of the class. There is still need for further studies on the anatomical details of the edrioasteroids, but well preserved specimens are so rare that further progress along this line must necessarily be slow.

It will be remembered that these primitive echinoderms, ranging from parasitic, circular expansions to elevated, sacklike bodies, free or attached by a part or all of the lower (aboral) surface, bear normally five straight or curved ambulacra (rays or arms) on their upper (oral) surface, arranged as follows: (1) left posterior (next to anal area); (2) left; (3) anterior (opposite anal area); (4) right; (5) right posterior. Usually, four of the ambulacra curve to the left (sinistral or counterclockwise), and the fifth (the right posterior) to the right (dextral or clockwise), the anal interradius thus occurring between the right and left posteriors. However, in some genera the rays are straight, or, again, they may all curve to the left or all to the right, or, as in the first established genus, *Agelacrinites*, three to the left and two to the right. Study of many specimens has shown that the direction and extent of curvature of the ambulacra, as well as the plate structure of the rays, the interradii or interambulacral areas, and the oral area, remain constant for the genus, but the number of ambulacra, although typically five, may vary in the same species just as in the modern starfishes.

<sup>1</sup> Smithsonian Misc. Coll., vol. 93, no. 8, pp. I-II, 1 pl., 1935.



In the list at the end of this paper only the articles dealing with the Edrioasteroidea in a more extensive way than the description of a species or two are cited. The bibliography of the American Ordovician and Silurian species can be found in the author's Bibliographic Index of 1915. For facility of reference the original generic name of the described species is inserted in parentheses. All the known species of the entire group are mentioned in this or the 1935 paper.

## Class EDRIOASTEROIDEA Billings, 1854-58

### Family STROMATOCYSTITIDAE, new family

*Stromatocystites* Pompeckj with its basal layer of plates and its allies *Walcottidiscus* Bassler and *Xenocystites*, new genus, are so different from the edrioasteroids with basal areas of attachment without plates that this new family seems necessary.

#### WALCOTTIDISCUS Bassler, 1935

Theca depressed, hemispherical to pentagonal globular, with five straight or curved ambulacra separated by polygonal interambulacral plates on the oral surface, and aboral surface completely covered by more or less polygonal plates.

Associated with the genotype, *W. typicalis* Bassler, is a second species possessing the same generic features, notably a theca as in *Stromatocystites*, but with curved ambulacra, four (1 to 4) directed to the left, and one, the right posterior (5), to the right. Better preserved specimens of this genus are necessary before the exact nature of the base can be determined, although the plate structure here appears to be as in *Stromatocystites*.

#### WALCOTTIDISCUS MAGISTER, n. sp.

Plate 2, fig. 2

The type specimen, a subpentagonal, depressed, semiglobular theca, 6 cm in diameter, apparently free, is, although crushed in hard shale and imperfectly preserved, sufficient to show that this is a magnificent species characterized by long, narrow, strongly curved ambulacra, four curved to the left and the right posterior to the right. The interambulacral areas are wide and occupied by large, polygonal, slightly imbricating plates, but the anal pyramid cannot be distinguished unless represented by a cluster of several small plates. The edge of the theca seems to be formed by small imbricating plates and

the under surface possibly by larger polygonal ones similar to the interambulacra.

Good examples of this interesting species would undoubtedly reveal a beautiful and remarkable structure for this early edrioasteroid. The large proportions, strongly curved ambulacra, and numerous large polygonal interambulacral plates readily distinguish it from the associated genotype.

*Occurrence*.—Middle Cambrian (Burgess shale), Burgess Pass, above Field, British Columbia (loc. 35k).

*Holotype*.—U.S.N.M. no. 90755.

#### STROMATOCYSTITES Pompeckj, 1896

In this genus the under surface of the theca is completely occupied by more or less regular polygonal plates, a feature so different from most other edrioasteroids that further studies of well-preserved material are much needed. Figures of the upper and lower surfaces of the genotype, *S. pentangularis* Pompeckj, from the Middle Cambrian of Bohemia, are reproduced on plate 1, figures 6, 7.

#### XENOCYSTITES, n. gen.

Theca a circular, depressed, hemispherical sack with the oral surface (although not directly observed) bearing five narrow, slightly curving ambulacra undoubtedly separated by many polygonal mosaic interambulacral plates (possibly eight rows at the periphery), and the basal side made up of similar, polygonal plates either completely covering this area or possibly leaving a small central opening marking the point of attachment. Anal area not observed. Basal covering plates of ambulacra long, narrow, in a single row.

*Genotype and only known species*.—*X. carteri*, new species. Chemung of New York.

#### XENOCYSTITES CARTERI, n. sp.

Plate 7, fig. 14

This interesting species is based upon a flattened circular disk, 45 mm in diameter, exposing the basal side of half of the theca which is covered with polygonal plates but shows the ambulacra clearly impressed upon these basal plates. Weathering exposing the under side of the plates of the oral surface indicates that they too are polygonal and mosaic and that the ambulacra have long, narrow basal floor plates in a single row. The central part of the base consists of a

mass of jumbled plates probably representing the under side of the oral area or possibly an opening in the basal layer. The direction of ambulacral curvature is uncertain, but two of the rays seem to curve slightly to the right.

The type and only known specimen collected by A. L. Carter, of Kenmore, New York, and kindly loaned for description by the New York State Museum, is so different from other edrioasteroids that this new genus is here defined, although the surface characters cannot actually be seen.

*Occurrence*.—Chemung (Gowanda), Cattaraugus Creek, Versailles, New York,  $\frac{1}{2}$  mile up creek from bridge.

*Holotype*.—Collection New York State Museum.

#### Family HEMICYSTITIDAE, new family

Theca composed of thin plates with an oral surface of five ambulacra separated by interambulacra and attached by the greater part of the aboral surface permanently or temporarily to some outside object. Oral covering plates three, one large plate next to the anal area with two smaller adjacent ones.

*Hemicystites* Hall, 1852, *Cystaster* Hall, 1871, *Cincinnatidiscus* Bassler, 1935, *Carneyella* Foerste, 1916, *Streptaster* Hall, 1872, *Lebetodiscus* Bather, 1908, *Foerstediscus* Bassler, 1935, and probably *Pyrgocystis* Bather, 1915, all agree in the very definite number and arrangement of the oral plates as well as the other characters mentioned above, so that this feature is believed to be of family importance.

#### CYSTASTER Hall, 1871

The view of the genotype *C. (Hemicystites) granulatus* (Hall) on plate 1, figure 14, clearly exhibits the generic characters, namely, a theca in the form of an attached elevated elongate sack with five short straight ambulacra, minute, fused, rounded or polygonal interambulacral plates in mosaic, small scalelike marginal plates, and a raised anal pyramid of very small nodose plates.

#### CYSTASTER ULRICHI, n. sp.

Plate 2, figs. 3-5

This species, named in honor of Dr. E. O. Ulrich, is based upon a single example about 4 mm in diameter attached to a ramose bryozoan. It differs from the genotype and only other known species in the shorter, broader sack forming the basal portion of the theca, and in

the coarser and fewer plates covering the ambulacral areas, there being two rows of 5 or 6 plates to each ambulacrum, in contrast to 9 or 10 in Hall's species. All plates show a punctate structure. The oral plates, one large and two small ones opposite it, are quite visible. Interambulacral plates minute, nodose; anal pyramid indistinct but visible.

*Occurrence*.—Cincinnatian (Eden shale-Economy beds), West Covington, Kentucky.

*Holotype*.—U.S.N.M. no. 42138.

#### CINCINNATIDISCUS Bassler, 1935

Species of this genus, formerly confused with *Hemicystites*, show most resemblance to *Cystaster* except that the theca is depressed or flat, attached by the whole basal surface, and the interambulacral plates are squamose, imbricating distinctly, and surrounded by a marginal zone of small nodose plates.

#### CINCINNATIDISCUS (HEMICYSTITES) STELLATUS (Hall), 1856

Plate 2, figs. 11, 12

This edrioasteroid, the type of the genus, is not so uncommon and thus affords opportunity for the study of specific variations. Figure 11 on plate 2 shows that the number of rays may vary as in other genera. The theca, averaging 8 mm in diameter, is attached, depressed, pentagonal, with usually five straight, short, broad, club-shaped rays bearing usually 12 covering plates to a row, each plate being almost as wide as long. Supraoral plates three, a large one opposite the anal area, and opposite this two smaller ones. Anal pyramid of very small nodose plates. Interambulacral plates imbricating, squamose, the central ones larger, and the outer marginal ones smaller and covered with small nodes.

*Occurrence*.—Cincinnatian (Maysville-Fairmount and Bellevue formations), Cincinnati, Ohio, and vicinity.

*Plesiotypes*.—U.S.N.M. no. 42106.

#### CINCINNATIDISCUS (HEMICYSTITES) CARNENSIS (Foerste), 1914

Plate 5, fig. 4

Theca discoidal, faintly pentagonal, 7 mm in diameter, with prominent rays, subclavate in outline, similar to *C. stellatus* (Hall) but differing in its narrower rays and correspondingly wider interambulacral areas.

*Occurrence*.—Trenton (*Strophomena vicina* zone), Carntown, Kentucky.

*Cotype*.—U.S.N.M. no. 87163.

**CINCINNATIDISCUS TURGIDUS, n. sp.**

Plate 5, fig. 12

Based upon a single specimen, 8 mm in diameter, associated with *Isorophus austini* (Foerste) encrusting a *Rafinesquina* shell. Except that the fifth ray has been destroyed, the theca is well preserved and shows the usual generic characters. The ambulacral covering plates, 10 to 12 to each row, are about as broad as in *C. stellatus* (Hall), but are much longer in the middle part of the ray, becoming considerably narrowed at the extremity, thus giving the ambulacra a swollen aspect. Although this is emphasized in the type specimen by the fact that the plates of several rays have been pulled apart slightly, nevertheless they are clearly wider in the midlength of a normal ray.

*Occurrence*.—Richmond (Whitewater formation), Oxford, Ohio.

*Holotype*.—U.S.N.M. no. 87628.

**CINCINNATIDISCUS EDENENSIS, n. sp.**

Plate 2, fig. 10; plate 3, fig. 11

Similar to *C. stellatus* (Hall) in general features, but differing in that the rays are broader and the ambulacral covering plates are much longer and so narrow, erect, and imbricating that they appear as sharp edges.

*Occurrence*.—Cincinnatian (Eden-McMicken beds), Cincinnati, Ohio.

*Holotype*.—U.S.N.M. no. 34413.

**CARNEYELLA Foerste, 1916**

Theca typically elevated, sacklike, attached by a broad basal part, but also of depressed parasitic disks; ambulacra curved, four to the left and the right posterior to the right. Oral area of three plates, one large, next to the anal region, and opposite these two small. Surface of plates minutely pitted but often ornamented with conspicuous nodes and ridges.

Three well-marked new forms here noted with four previously known, ranging from the base of the Trenton through the Richmond, give this genus a good representation and range. *C. (Agelacrinus)*

*pileus* (Hall), the genotype, forms hemispherical sacks about 15 mm wide and 5 mm high, attached by a broad base, in which the surface ornamentation other than the minute punctations is wanting save on the marginal plates. *Carneyella* (*Lebetodiscus*) *platys* (Raymond), 1915 (pl. 7, fig. 15), from the Trenton of Canada, and *C. raymondi* Clark, 1919, from the Trenton of New York, are referred to the genus with doubt.

**CARNEYELLA (AGELACRINUS) VETUSTA (Foerste), 1914**

Plate 2, fig. 14

This species is refigured to show that the papillose surface ornament of the plates is a part of the theca and not an incrusting hydroid like *Dermatostroma*, as once believed. Such surface ornamentation, although very well developed here, occurs in various degrees in all species of the genus and, indeed, forms one of the generic characters. The very short, much curved ambulacra and the broad band of highly nodose marginal plates in connection with the depressed disk form of the theca, and the many papillae hiding the outlines of the plates, are the specific characters.

*Occurrence*.—Trenton (Cynthiana formation), Clay's Ferry, 14 miles southeast of Lexington, Kentucky.

*Holotype*.—U.S.N.M. no. 87162.

**CARNEYELLA NICKLESI, n. sp.**

Plate 2, fig. 13

This well-characterized new species, named in honor of John M. Nickles, bibliographer of American geology, is distinguished at once from all others of the genus by its long, broad, much curved ambulacra, with about 20 short, wide covering plates in each row, and by the large, slightly imbricating, plainly visible interambulacral plates not obscured by surface ornamentation, which in this case consist of minute papillae arising from the finely punctate surface.

*C. cincinnatiensis* Bassler (pl. 2, fig. 15) has a similarly depressed theca and surface ornamentation, but here there are fewer covering plates to a row, the ambulacra curve less strongly, and the whole appearance is less robust.

*Occurrence*.—Trenton (Curdsville limestone), near Troy, Woodford County, Kentucky.

*Holotype*.—U.S.N.M. no. S-3191.



**CARNEYELLA ULRICHI, n. sp. (Bassler and Shideler)**

Plate 6, figs. 5, 6

Theca an elevated sack about 20 mm wide and 10 mm high, with the general features of *C. pileus*, but differing decidedly in the very spinous surface ornamentation of the plates. In both species the plates are minutely punctate, but in *C. ulrichi* each plate bears at least one round, swollen pustule ending in a sharp, pointed spine, and the larger plates have a number of such elevations all sharply marked and distinct from each other. Each of the ambulacral plates bears a sharp, rounded spine on the outer half and a similar elevation emerges from the inner edge. The interambulacra have one to four such spines, and each of the larger elongate marginal plates sometimes bears several dozen. Each of the outermost series of small plates has a single spine in the center.

This and the following new species, as well as several other species herein described, were discovered by Dr. W. H. Shideler and generously presented to the National Museum. The writer has included Dr. Shideler as coauthor of these two species, since both of us wish to name them in honor, respectively, of Drs. Ulrich and Foerste, whose knowledge of the edrioasteroids as well as of other groups has always been at our service.

*Occurrence*.—Cincinnati (Maysville-Bellevue formation), railroad cut, south of Maysville, Kentucky.

*Holotype*.—U.S.N.M. no. S-3964.

**CARNEYELLA FOERSTEI, n. sp. (Bassler and Shideler)**

Plate 6, figs. 7, 8

This well marked species of the *C. pileus* group is similar to the preceding in its general characters but differs in its more robust theca and broader, longer, more developed ambulacra, and particularly in the surface ornament. Each of the ambulacral plates has one to four round pustules on the broad end next to the interambulacral area and a single ridgelike elevation longitudinally arranged along the rest of the plate. Elsewhere one to a dozen round pustules rise from each of the finely punctate plates, whereas in *C. ulrichi* the corresponding elevations are sharp-pointed spines.

*Occurrence*.—Richmond (Arnheim formation), Russellville, Ohio.

*Holotype*.—U.S.N.M. no. S-3965.



**CARNEYELLA (AGELACRINUS) FABERI (Miller), 1894**

Dr. Foerste has refigured the type of this species, stating that it is too poorly preserved to merit description but that the occurrence of numerous tubercles on the plates suggests relationship to *Carneyella*. It is, therefore, probable that the species can be held as valid when similarly ornamented and more complete specimens from this horizon are found.

*Occurrence*.—Richmond (Whitewater formation), between Osgood and Versailles, Indiana.

**STREPTASTER Hall, 1872**

This genus is well characterized by the sinistral curvature of all its rays and by the small polygonal interambulacral plates forming a mosaic. The number of ambulacra, although normally five, varies. *S. (Agelacrinus) septembrachiata* (Miller and Dyer) more often has five rays instead of seven as in the type. Specimens of *S. reversata* Foerste, more complete than the original, which has one ray reversed, will probably show it to be better placed in *Carneyella*.

**LEBETODISCUS Bather, 1908**

As shown by the genotype, *L. (Agelacrinites) dicksoni* (Billings), 1857 (pl. 1, fig. 11), all five ambulacra are directed toward the left, resembling *Streptaster* in this respect, but the latter has strongly curving arms closely arranged and lacks the large mosaic interambulacral plates.

**LEBETODISCUS LORIFORMIS Raymond, 1915**

Plate 3, fig. 10

A view of the type specimen of this species is here introduced to show the relationship of the genus to *Carneyella*, differing in that all of the ambulacra curve strongly to the left and that large mosaic interambulacral plates separate the rays.

*Occurrence*.—Middle Trenton (Cystid beds), Ottawa, Ontario.

*Plastotype*.—U.S.N.M. no. S-3882. Original in Victoria Memorial Museum, Ottawa.

**FOERSTEDISCUS Bassler, 1935**

Three well marked species, the genotype *F. grandis* Bassler, 1935, from the Trenton of Kentucky, and the two herein described, agree exactly in the dextral curvature of all the arms and the mosaic

arrangement of the interambulacra, the essential generic characters. *Cooperidiscus* has a similar arrangement of ambulacra, but the interambulacra are highly imbricated.

**FOERSTEDISCUS SPLENDENS, n. sp.**

Plate 7, fig. 13

The theca, a depressed semiglobose sack about 3 cm in diameter resting upon a limestone layer, is very similar to the genotype in its general characters but differs decidedly in the greater length of its much more curved ambulacra, which in addition have more numerous plates in each row. The anal pyramid also differs in that here it is a narrow elevated tube instead of a flat broad area of small plates as in *F. grandis*.

The type specimen, a splendid example of these rare fossils, collected by Irving G. Reimann, was obtained for description through the courtesy of Dr. C. R. Stauffer, of the University of Minnesota.

*Occurrence*.—Black River (Decorah shale, top of *Rhinidictya* bed), Ford plant, St. Paul, Minnesota.

*Holotype*.—U.S.N.M. no. S-4079.

**FOERSTEDISCUS PARVUS, n. sp.**

Plate 2, figs. 6, 7

This species, represented by a dozen examples all exactly similar to the two cotypes figured, differs from the genotype in the small size of the theca, about 6 mm in diameter, the general delicacy of its parts, and the more imbricating nature of its interambulacral plates. The strongly curved ambulacra all directed to the right, and the anal area composed of small irregularly arranged plates, are generic features common to the two species.

*Occurrence*.—Trenton (Hull formation), Kirkfield, Ontario.

*Cotypes*.—U.S.N.M. no. S-3889.

**PYRGOCYSTIS Bather, 1915**

This genus, introduced here for sake of completeness, is described and its component species listed in our 1935 paper. The theca is a high cylindrical turret of overlapping plates surmounted by the oral surface with five broad straight ambulacra.

**HEMICYSTITES Hall, 1852**

The writer has shown that this genus, usually associated with the structure shown in *Cincinnatidiscus* (*Agelacrinus*) *stellatus* (Hall),

is in reality, according to its genotype, *H. parasiticus*, a *Carneyella* with broad, short, straight ambulacra and with squamose imbricating overlapping plates. The genus is the most prolific of all the edrioasteroids so far known. New figures of the genotype and of several previously known species referred to other genera, as well as illustrations of Barrande's species (pl. 7, figs. 2-6), are introduced here in addition to the description of several new species.

#### HEMICYSTITES PARASITICUS Hall, 1852

Plate 4, figs. 5, 6

The original figure is diagrammatic, as it is based upon a somewhat crushed and broken specimen, but comparison of the type with a complete example from the same horizon and locality shows the generic as well as specific features of the species. The ambulacra are short, broad, and straight, with numbers 1 and 5, between which the anal pyramid is located, diverging at a wider angle than the rest. The interambulacral plates are elongate, polygonal, imbricating, and the marginal rows of plates, six or seven in number, increase in size from a row of minute ones at the edge to a row composed of large plates encircling the ambulacra. The anal area is large, consisting of six or seven elongate triangular plates meeting in pyramid form.

*Occurrence*.—Clinton (Rochester shale), Lockport, New York.

*Plesiotype*.—U.S.N.M. no. S-3183.

#### HEMICYSTITES (LEBETODISCUS) MULTIBRACHIATUS (Raymond), 1915

Plate 4, figs. 3, 4

The holotype of this species (fig. 3) is surely an abnormal individual in which the original five ambulacra have been increased to eight by branching of numbers 1, 2, and 4. The same locality affords very similar specimens with the normal five ambulacra (fig. 4), for which reason such specimens are included under the same name irrespective of the number of arms in the type. *H. multibrachiatus* can be recognized by its short, widely separated straight ambulacra with seven to eight covering plates to a row, surrounded by a broad band of rather nodose, imbricating plates.

*Occurrence*.—Trenton (Hull formation), Kirkfield, Ontario.

*Plesiotype*.—U.S.N.M. no. S-3894.

#### HEMICYSTITES (LEBETODISCUS) CHAPMANI (Raymond), 1915

Plate 3, fig. 9

This very beautiful species is remarkable for the length of the ambulacral areas, which are broad in the oral region and taper gradu-

ally, with about 15 covering plates to a row, all arched along the median line of junction. The species is so much like *H. rectiradiatus* (Shideler) (pl. 5, fig. 10) from the Richmond group that differences are hard to note. When magnified to the same diameter and compared, *H. rectiradiatus* seems to have slightly longer, narrower, less tapering ambulacra. Related also to *H. youngi*, it differs in having longer, more slender rays.

*Occurrence*.—Trenton (upper part *Prasopora* zone), near Jackson Park, Peterborough, Ontario.

*Plastotypes*.—U.S.N.M. no. S-3892. Originals in Victoria Memorial Museum, Ottawa.

#### HEMICYSTITES (LEBETODISCUS) YOUNGI (Raymond), 1915

Plate 3, fig. 1

Although probably related to *H. chapmani* (pl. 3, fig. 9), the relatively shorter and broader rays will distinguish *H. youngi*. Compared with *H. billingsi*, a very similar species, *H. youngi* differs in the broader rays and in lacking the large punctate marginal plates. The short, wide ambulacra and the unusual size and length of the ambulacral covering plates, as well as the overlapping interambulacra, readily characterize this species.

*Occurrence*.—Middle Trenton, Eldon Township, Victoria County, Ontario.

*Plastotype*.—U.S.N.M. no. S-3896. Original in Victoria Memorial Museum, Ottawa.

#### HEMICYSTITES (AGELACRINUS) BILLINGSI (Chapman), 1860

Plate 3, fig. 2

The photograph on plate 3 of Raymond's plesiotype of this species indicates a *Hemicystites* similar to *H. (Lebetodiscus) youngi* (pl. 3, fig. 1) but distinguished by its larger marginal and interambulacral plates, its shorter rays, and by the pitted condition of all the plates.

*Occurrence*.—Trenton (Cystid beds), near Jackson Park, Peterborough, Ontario.

*Plastotype*.—U.S.N.M. no. S-3891. Original in Victoria Memorial Museum, Ottawa.

#### HEMICYSTITES CURTUS, n. sp.

Plate 4, fig. 8

This minute species, which occurs as a slightly convex theca about 6 mm in diameter attached to a limestone slab, may be distinguished

at once by the large size of its three oral plates and the very short, broad, rapidly tapering ambulacra with only four or five covering plates in a row. Other features are the well-developed anal pyramid occupying a considerable portion of the interambulacral area, and the row of very large plates immediately encircling the tips of the ambulacra. The other rows of encircling plates and the interambulacral plates are small in contrast.

*Occurrence*.—Black River (Platteville limestone), Rockton, Illinois.

*Holotype*.—U.S.N.M. no. 42105.

#### HEMICYSTITES GERMANUS, n. sp.

Plate 4, fig. 7

Although apparently closely related to *H. curtus* in its short, broad ambulacra, the two individuals attached to a brachiopod shell on which the present species is based differ in that the covering plates are smaller and more numerous in each ambulacral row, and the encircling rows of marginal plates are less differentiated, smaller, and more imbricating.

*Occurrence*.—Trenton (Catheys formation), Love Branch, Maury County, Tennessee.

*Cotypes*.—U.S.N.M. no. 42140.

#### HEMICYSTITES PAULIANUS, n. sp.

Plate 4, fig. 9

In general aspect this species is very similar to *H. germanus*, from which it differs, however, in that the ambulacra are longer, taper more slowly, and contain more covering plates in each row.

*Occurrence*.—Black River (Decorah shale, *Phylloporina* bed), St. Paul, Minnesota.

*Holotype*.—U.S.N.M. no. 42114.

#### HEMICYSTITES RICHMONDENSIS, n. sp.

Plate 5, figs. 5-7

Theca small, averaging 7 mm in diameter, with ambulacra short, straight, wide, not narrowing much toward their extremity, bearing 6 to 8 plates in each row, and surrounded by a broad rim of punctate, wide plates, and then by several marginal rows of smaller plates.

This rather widespread Richmond species differs from the associated *Isorophus austini* in that the arms are broad and straight instead

of narrow and curved, and in the three large oral plates characteristic of the genus instead of numerous small ones. It is not the young of some other edrioasteroid because the numerous specimens discovered all maintain the same maximum size with the typical structure of the genus.

*Occurrence*.—Richmond, Warren County, Ohio, and Versailles, Indiana (Waynesville formation), Oxford, Ohio (Liberty), and Adams County, Ohio (Whitewater).

*Cotypes*.—U.S.N.M. nos. 40742, 42111, 68333.

**HEMICYSTITES (AGELACRINITES) RECTIRADIATUS (Shideler), 1918**

Plate 5, fig. 10

The type specimen of this magnificent species is a flattened theca about 18 mm in diameter attached to a clay pebble. It is characterized by long, narrow, straight arms tapering only at their extremity, separated by wide interambulacral areas covered by large polygonal, little imbricating plates and with an oral area of one large and two small plates, all encircled by a broad band of marginal plates, very large in the inner row and small around the edge. Comparison with the very similar *H. chapmani* is noted under that species.

*Occurrence*.—Richmond (Lower Whitewater), Olive Branch, Harshville, Adams County, Ohio.

*Holotype*.—U.S.N.M. no. S-3954.

**HEMICYSTITES DEVONICUS, n. sp.**

Plate 7, fig. 1

Theca small, 6 mm in diameter, attached to a *Chonetes*. The interambulacral and oral plates are rather large and somewhat disturbed, but show distinctly that the rays are exceptionally short, straight, broad at the oral end, and taper very rapidly, with only 4 or 5 plates to a row. Other features as in the genus. The very short, rapidly tapering ambulacral rows distinguish this species from all others of the genus.

*Occurrence*.—Devonian (Long Lake beds), abandoned shale pit of Alpena Portland Cement Company, Alpena County, Michigan.

*Holotype*.—Collection Geological Department, University of Michigan, no. 17295.



**HEMICYSTITES (?) CARBONARIUS, n. sp.**

Plate 4, figs. 10, 11

This curious edrioasteroid occurs as thin, parasitic disks, the largest 11 mm in diameter, attached to a smooth cephalopod shell. The ambulacral areas although radiating straight from the center are obscured as to their detailed structure. This radiate arrangement and the aspect of the encircling rows of plates are so like *Hemicystites* that the species can be referred there at least provisionally. Young specimens show even less definite arrangement of the ambulacral plates than mature examples.

*Occurrence*.—Pennsylvanian (Bluefield shale), railroad cut  $\frac{1}{3}$  mile east of Addis Valley, West Virginia.

*Cotypes*.—U.S.N.M. no. 91837.

**Family AGELACRINITIDAE Bassler, 1935**

Theca as in the Hemicystitidae except that the plates covering the oral area are small, numerous, and without any definite order. A single row of ambulacral flooring plates overlapping proximally.

*Agelacrinites* Vanuxem, 1842, *Isorophus* Foerste, 1916, *Isorophusella* Bassler, 1935, *Thresherodiscus* Foerste, 1914, *Discocystis* Gregory, 1897, *Cooperidiscus* Bassler, 1935, *Ulrichidiscus* Bassler, 1935, and *Lepidodiscus* Meek and Worthen, 1868, are placed in this family as restricted, the arrangement of the oral covering and ambulacral flooring plates being regarded as important characters.

**THRESHERODISCUS Foerste, 1914**

In this genus the branching of the ambulacral rays is carried to an extreme as shown in the illustration of the oral side of *T. ramosus* Foerste, the genotype and only species from the Lower Trenton of Manitoulin Island, Lake Huron (pl. 2, fig. 8). The illustration shows also that the rays have a pronounced trimerous origin which is perhaps the condition existing in many of the edrioasteroids. The interambulacral plates are large and squamose, imbricating in the central part and smaller along the border.

**AGELACRINITES Vanuxem, 1842**

This genus, fairly well represented in the Upper Paleozoic of both America and Europe, is readily recognized by its five long, narrow, much curved ambulacra, two of which (4 and 5) bend to the right, and three (1, 2, 3) to the left, and by the sculptured, mosaic inter-



ambulacral plates. The genotype, *A. hamiltonensis* Vanuxem (pl. 1, fig. 18), originally figured in a reversed position, is a handsome fossil of the Hamilton group of New York. *A. rhenanus* Roemer, 1851, from the Devonian of Germany, selected as genotype of *Haplocystites* by Roemer and later changed to *Haplocystis* by Bather (pl. 1, figs. 12, 13), proves to be founded upon a mould of the underside of part of the oral disk of a typical *Agelacrinites*. *A. blairi* Miller, 1894, from the Warsaw limestone at Boonville, Missouri, was incorrectly figured since the type specimen shows that the rays curve as in typical *Agelacrinites* (pl. 7, fig. 9). *A. legrandensis* Miller and Gurley, 1894, was based upon a mutilated specimen showing only four ambulacra, but our illustration (pl. 4, fig. 13) of an excellent example in the Springer collection from the same horizon and locality, shows a normal number and arrangement of the ambulacra.

**AGELACRINITES SOUTHWORTHI, n. sp.**

Plate 4, fig. 12

This handsome species is based upon a specimen perfect in all details except that the left posterior ray and the adjoining interambulacral plates are slightly crushed and in part destroyed. As our photograph shows, the structure of the rays is similar to that in the genotype, but their length falls far short since they end a little distance beyond their angle of curvature. The interambulacral plates, which are large, smooth, and imbricating, differ markedly from the sculptured polygonal, very slightly overlapping plates of the genotype. A closer relative is perhaps *A. hanoveri* Thomas (pl. 7, fig. 10) from the Shell Rock division of the Devonian at Mason City, Iowa, in which the ambulacra are very similar, but a ridge composed of the inner rows of encircling plates is present, and the arms are still shorter.

The specific name is in honor of Charles Southworth, of Thedford, Ontario, whose researches in the Hamilton rocks of Ontario have brought to light many fine fossils.

*Occurrence*.—Hamilton (Arkona beds, 20 to 30 feet below the Encrinal limestone), Marsh's Mill, Arkona, Ontario.

*Holotype*.—U.S.N.M. no. S-3478.

**ISOROPHUS Foerste, 1916**

In this genus the oral area is covered by numerous small plates and an extra series of ambulacral covering plates often occurs between the usual two rows. The interambulacral plates, scalelike and more or

less imbricating, and the circular depressed attached theca with ambulacral rays 1 to 4 curving to the left and 5 to the right, are other features of the genus. *I. (Agelacrinus) cincinnatiensis* (Roemer) (pl. 5, fig. 11), the genotype, and one of the less rare of the edrioasteroids, was originally figured with the rays curving in the opposite direction, but this was due to reversal of the image produced in drawing with the camera lucida of that time. Wherever noted, young specimens of *Isorophus* exhibit short, less curved rays and a broader oral area than in the mature forms.

**ISOROPHUS TENNESSEENSIS, n. sp.**

Plate 2, fig. 1

Theca a thin disk about 8 mm in diameter adherent to a brachiopod shell (*Rafinesquina*). The species has the ambulacral and oral plate arrangement of the genus, but with the oral area rather broad and composed of an unusually large number of small plates and the ambulacra shorter than usual although strongly curved. The small theca, rather narrow, short, much curved ambulacra, large oral area, and broad rim of marginal plates characterize this species. *I. trentonensis*, new species, from the Trenton limestone of New York, is similar but has shorter, wider little curved rays, and the oral covering plates are larger.

*Occurrence*.—Trenton (shaly beds in Cannon limestone), Fayetteville, Tennessee.

*Holotype*.—U.S.N.M. no. 91839.

**ISOROPHUS TRENTONENSIS, n. sp.**

Plate 5, fig. 1

As noted under *I. tennesseensis*, this new species differs in its short, broad, almost straight, bluntly terminating arms, and in the larger size of the plates forming the broad oral area. Enlarged photographs bring out these differences clearly.

*Occurrence*.—Trenton (upper part of Deltoidea zone), Trenton Falls, New York.

*Holotype*.—U.S.N.M. no. 91843.

**ISOROPHUS (AGELACRINUS) AUSTINI (Foerste), 1914**

Plate 2, fig. 9; plate 6, figs. 1, 2

This neat species is so small, (about 8 mm in diameter) that it might be mistaken for the young of the larger edrioasteroids, but the

photographic illustrations show it to have characteristics of typical mature *Isorophus*, differing from other species in the delicacy of its parts and its short, narrow recurved rays. One of the original types and a specimen more robust than usual, as well as an example showing the under side of the theca, are here illustrated.

*Occurrence*.—Richmond (Whitewater formation), Dutch Creek,  $4\frac{1}{2}$  miles northwest Wilmington, Ohio, Fallen Timbers Creek, Versailles, Indiana, and Dodge's Creek, Oxford, Ohio.

*Cotypes and plesiotypes*.—U.S.N.M. nos. 70162, S-3961, S-3963.

**ISOROPHUS (AGELACRINUS) HOLBROOKI (James), 1878**

Plate 5, figs. 8, 9

This, the most striking species of the genus, is characterized by its large size (diameter, 30-40 mm), semiglobose to hemispherical shape, numerous rows of little imbricating interambulacral plates, and the long, comparatively narrow, ambulacra recurving strongly along the edge of the theca.

*Occurrence*.—Richmond (Arnheim formation), Morrow, Ohio.

*Plesiotype*.—U.S.N.M. no. 40744.

**ISOROPHUS GERMANUS, n. sp.**

Plate 6, figs. 3, 4

Closely related to *I. holbrooki* and probably a derivative of it, agreeing in its semiglobose theca (20 mm wide) and other characters, but differing in the fewer number of plates in all the interambulacral areas and in the less definite arrangement of the anal plates.

*Occurrence*.—Richmond (Waynesville-Clarksville division), Morrow and Oxford, Ohio.

*Cotypes*.—U.S.N.M. nos. S-3959, S-3960.

**ISOROPHUS KENTUCKYENSIS, n. sp.**

Plate 6, fig. 10

Theca a subhemispherical disk 25 mm in diameter, with the general characters of *Isorophus* and related to *I. holbrooki* but differing in that the arms are shorter, less recurved, and the interambulacral plates are smaller, less regular, and more imbricating.

Although undoubtedly a new species, the type specimen is crushed and not well enough preserved to show the fine details of the surface.

*Occurrence*.—Trenton (contact between Woodburn-Greendale formations), Lair Station, Kentucky.

*Holotype*.—U.S.N.M. no. S-3967.

**ISOROPHUS SHIDELERI, n. sp.**

Plate 6, fig. 9

This well-marked species with a theca 17 mm in diameter, equal to the usual width in the genus, is readily recognized by its long, much curved, extremely narrow rays made up of unusually small plates and separated by many comparatively small interambulacral plates. The marginal rim also, although broad, is composed of many rows of small plates. Curvature of arms, structure of oral and anal areas, and accessory plates on the ambulacra as in typical *Isorophus*.

The specific name is in honor of Prof. W. H. Shideler, of Miami University, who has collected a number of the best edrioasteroids herein described.

*Occurrence*.—Richmond (Elkhorn formation), just west of Hamburg, Indiana.

*Holotype*.—U.S.N.M. no. S-3958.

**ISOROPHUS (AGELACRINUS) WARRENENSIS (James), 1883**

Plate 5, figs. 2, 3; plate 6, fig. 11

The type of this species was poorly selected because in it the large interambulacral plates are sufficiently displaced by pressure to hide the ambulacra. Better specimens in the original lot, of which plate 5, figure 2, represents one, show this to be a good species characterized by its small diameter (13 mm) short, broad, slightly curved ambulacra, large polygonal, slightly overlapping interambulacral plates, broad oral area of numerous large plates, and wide marginal rim of large and small plates. The dozen or more specimens in the original lot maintain these characters as do specimens from other localities at the same horizon. The jumbled condition that the plates may assume is shown in plate 6, figure 11.

*Occurrence*.—Richmond, Oregonia, and near Morrow, Ohio (probably basal Arnheim formation); Clarksville, Ohio (Waynesville formation).

*Holotype and plesiotype*.—U.S.N.M. no. S-3957.

**ISOROPHUSELLA Bassler, 1935**

The large specimen of the genotype, *I. (Lebetodiscus) incondita* (Raymond), figured by the writer in 1935, very distinctly showed the

generic characteristics, three rays curved to the left and two to the right. Smaller, young examples, such as the type itself, have rays less curved, and in still younger specimens the rays are almost straight. A view of the specimen on the type slab showing the anal pyramid well preserved is represented on plate 7, figure 12, where the rays, although almost straight, show a tendency to curve left and right as in the older examples. The other characters of the genus are those of typical *Isorophus*. Typical *Agelacrinites* has the same arrangement of arms as in *Isorophusella*, but its sculptured mosaic interambulacral plates will readily distinguish it.

#### LEPIDODISCUS Meek and Worthen, 1868

Theca with the curvature of the ambulacra as in *Discocystis*, namely, four rays to the left and one to the right, but differing in the presence of strongly imbricating interambulacral plates. Or again, the genus resembles *Cooperidiscus* except that four of its ambulacra curve to the left instead of five to the right. In addition to *L. (Agelacrinites) squamosus* (Meek and Worthen), the genotype, (pl. 1, fig. 17), *L. (Agelacrinites) beecheri* (Clarke), *L. (Agelacrinites) buttsi* (Clarke) (pl. 7, fig. 8), *L. (Agelacrinites) lebouri* (Sladen) (pl. 1, fig. 19), and *L. milleri* Sharman and Newton (pl. 7, fig. 7), all from the Lower Carboniferous rocks, exhibit the curvature of ambulacra and imbricating interambulacrals characteristic of the genus. The following new species from the Middle Devonian is thus the earliest known.

#### LEPIDODISCUS ALPENENSIS, n. sp.

Plate 3, fig. 3

The type and only specimen, a theca about 7 mm in diameter, attached to a large *Chonetes*, shows clearly four ambulacra curved to the left and the fifth, the right posterior, to the right, as well as the strongly imbricating plates of typical *Lepidodiscus*. The anal pyramid, although somewhat broken, is large and occupies a central position between the left and right posterior rays. The small size and the combination of characters diagnostic of the genus will separate this species from other Devonian edrioasteroids.

*Occurrence*.—Devonian (Traverse group-Presque Island division of Long Lake formation), Quarry of the Alpena Portland Cement Company, Alpena County, Michigan.

*Holotype*.—Collection Geological Department, University of Michigan, no. 17296.

**DISCOCYSTIS Gregory, 1897**

This genus, of which three well-marked species are now known, exhibits the essential characters of *Agelacrinites* except that four of the ambulacra are curved to the left and one, the right posterior, to the right, and the theca is more sacklike, with many rows of closely imbricated marginal plates. The genotype, *Echinodiscus optatus* Worthen and Miller (pl. 1, fig. 5), was based upon the basal side of a specimen of *D. (Agelacrinites) kaskaskiensis*. Besides the genotype and the following new species, the genus includes *D. (Echinodiscus) sampsoni* (Miller), 1891, from the Warsaw of Missouri.

**DISCOCYSTIS LAUDONI, n. sp.**

Plate 3, figs. 7, 8

This fine species, the types of which were collected and presented by Dr. L. R. Laudon, of Tulsa University, is readily distinguished by its narrow, well-developed long ambulacra curving decidedly throughout their length. In *D. sampsoni* and *D. kaskaskiensis* the ambulacra are comparatively straight for the first third of their length and then curve rather abruptly. In other features these three species show the generic characters very uniformly.

*Occurrence*.—Kinderhook (Gilmore City formation), Gilmore City, Iowa.

*Cotypes*.—U.S.N.M. no. S-3886.

**DISCOCYSTIS (AGELACRINUS) KASKASKIENSIS (Hall), 1858**

Plate 1, figs. 4, 5; plate 3, figs. 4-6; plate 7, fig. 11

*Agelacrinites kaskaskiensis* HALL, Geol. Iowa, vol. 1, pt. 2, p. 696, pl. 25, fig. 18, 1858.

*Echinodiscus optatus* WORTHEN and MILLER, Geol. Surv. Illinois, vol. 7, p. 336, pl. 18, fig. 3, 1883.

The original type of this species failed to show clearly the direction of curvature of the fifth arm, so Hall's illustration is here corrected (pl. 1, fig. 4). The great width of the zone of marginal plates (pl. 1, fig. 5, pl. 7, fig. 11) restricts the attached part of the theca to a small circular central opening. Specimens with an abnormal number of arms occur here as in other edrioasteroids, as shown on plate 3, figure 5. The covering floor plates of the ambulacra are in distinct uniserial rows (pl. 3, fig. 6).



*Occurrence*.—Chester group, Kaskaskia, Illinois (*D. kaskaskiensis*), Polk County, Missouri (*E. optatus*), Huntsville, Alabama (Ste. Genevieve limestone), and Grayson County and Sloans Valley, Kentucky (Glen Dean).

*Plesiotypes*.—U.S.N.M. nos. S-3883, S-3884.

#### ULRICHIDISCUS Bassler, 1935

Ambulacra all curve strongly to the left with slightly imbricated interambulacrals. *Lebetodiscus* has similar curvature, but the interambulacrals are mosaic.

*Genotype and only known species*.—*U. (Agelacrinus) pulaskiensis* (Miller and Gurley) from the Mississippian (Chester) of Kentucky.

#### COOPERIDISCUS Bassler, 1935

Theca and general characters as in *Ulrichidiscus*, but all the rays curve to the right and are separated by closely imbricating interambulacrals. *Foerstediscus* has a similar curvature, but the interambulacrals are mosaic.

*Genotype and only known species*.—*C. (Lepidodiscus) alleganius* (Clarke) from the Devonian (Chemung) of New York.

#### Family EDRIOASTERIDAE Bather

This family was founded on the character of the ambulacra, which were so strongly developed that they passed on to the aboral surface. However, this seems to be a minor feature since the dividing line between the upper and lower surface may be questionable. The occurrence of the ambulacral flooring plates in two rows is a more definite character.

Illustrations of the genotype of *Edrioaster* Billings, 1858 (pl. 1, fig. 1) and of *Dinocystis* Bather, 1898 (pl. 1, figs. 2, 3), the latter probably belonging to the family are introduced here for comparative purposes.

#### Family CYATHOCYSTIDAE Bassler

In this family the number of rows of marginal plates has been increased to such an extent that they form a solid, fused, more or less cone-shaped mass attached at the aboral end to some foreign object, and bearing the ambulacra at the top or free end. Two genera have been distinguished, *Cyathocystis* Schmidt, 1880, with an oral surface much as in *Stromatocystites*, and *Cyathotheca* Jaekel, 1927, in which the ambulacral areas are apparently so narrow that they are



practically hidden at the surface. *Cyathotheca suecica* Jaekel, 1927 (pl. 1, fig. 10) from the Ordovician of Sweden, and *C. (Cyathocystis) corallum* (Jaekel) 1918, occurring in the Ordovician of Russia, are the known representatives of this genus, whereas in addition to the genotype, *C. plautinae* Schmidt, 1880 (pl. 1, figs. 8, 9) and *C. rhizophora* Schmidt, 1880, from the Ordovician of Estonia, *Cyathocystis* is represented by the following closely allied new American species.

**CYATHOCYSTIS AMERICANUS, n. sp.**

Plate 4, fig. 1, 2

This new species, although closely allied to the European forms, known to the writer only from the rather diagrammatic drawings of Dr. Schmidt, seems to differ decidedly in the fact that the ambulacra are much broader, shorter, and taper more rapidly. The type and only specimen exhibits a subpentagonal theca with the base drawn out into rootlike processes by which it was attached. The oral surface is slightly convex, but a portion is broken away so that the anal area is not visible. The discovery of this genus in America is another bit of evidence as to the European origin of this east Tennessee Chazyan fauna.

*Occurrence.*—Chazyan (Blount group-Ottosee formation), Knoxville, Tennessee.

*Holotype.*—U.S.N.M. no. 91846.

POSITION UNCERTAIN

Certain genera which have been considered edrioasteroids in the past should now be definitely eliminated. These are *Astrocystites* Whitcaves, 1897 (pl. 1, figs. 15, 16), and *Cyclocystoides* Billings and Salter, 1858, and its allies.

Although Bather recognized *Astrocystites* as an edrioasteroid, Hudson (1925) concluded that this genus was a true blastoid and was nearer *Pentremites* than either *Asteroblastus*, *Asterocystis*, or *Blas-toidocrinus*. These four genera are represented by so few specimens that pending further discoveries, they might well be assigned to the Protoblastoidea, the first order of blastoids.

The family Cyclocystoididae, however, does not belong to this category and must be left at present as an uncertain order of Pelmatozoa.

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## EXPLANATION OF PLATES

## PLATE I

(All figures after the respective authors of the species unless otherwise stated.)

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## PLATE 2

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Cincinnati (Maysville-Fairmount and Bellevue): Cincinnati, Ohio.	
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## PLATE 3

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- FIGS. 4-6. *Discocystis (Agelacrinus) kaskaskiensis* (Hall)..... 21  
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 Chester (Ste. Genevieve): Huntsville, Alabama.
6. Aboral side of theca,  $\times 1.3$ , showing the narrow opening of the attached portion, the fused plates of the basal surface, the mosaic arrangement of the interambulacrals, and the single row of flooring ambulacral plates.  
 Chester (Glen Dean): Grayson County, Kentucky.
- FIGS. 7, 8. *Discocystis laudoni*, new species..... 21
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 8. Another specimen,  $\times 1.3$ , exhibiting the anal area and its encircling ambulacra more clearly.  
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- FIG. 9. *Hemicystites (Lebetodiscus) chapmani* (Raymond)..... 11, 12  
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- FIG. 11. *Cincinnati discus edenensis*, new species..... 6  
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#### PLATE 4

- FIGS. 1, 2. *Cyathocystis americanus*, new species..... 23  
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|--|------|
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| Trenton (Hull formation): Kirkfield, Ontario.  |      |
| FIGS. 5, 6. <i>Hemicystites parasiticus</i> (Hall).....  | 11   |
| 5. The holotype, $\times 4$ , clearly identical, although broken, with the following.  |      |
| 6. A complete specimen, $\times 4$ , consisting of a thin, flattened disk attached to a <i>Spirifer</i> , with characteristic short, broad, straight ambulacra and large anal pyramid.                                     |      |
| Clinton (Rochester shale): Lockport, New York.   |      |
| FIG. 7. <i>Hemicystites germanus</i> , new species.....  | 13   |
| Two examples, $\times 4$ , of this minute species attached to a <i>Rafinesquina</i> . The quickly tapering ambulacra with small plates and the broad oral area are characteristic.   |      |
| Trenton (Catheys): Love Branch, Maury County, Tennessee.   |      |
| FIG. 8. <i>Hemicystites curtus</i> , new species.....  | 12   |
| The type, $\times 4$ , a beautifully preserved small disk attached to a limestone slab. The ambulacra are exceptionally short and broad and the ambulacral plates larger than usual.                                       |      |
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| FIG. 9. <i>Hemicystites paulianus</i> , new species.....   | 13   |
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| Black River (Decorah shale): St. Paul, Minnesota.  |      |
| FIGS. 10, 11. <i>Hemicystites (?) carbonarius</i> , new species.....   | 15   |
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| Pennsylvanian (Bluefield shale): Railroad cut, $\frac{4}{5}$ mile east of Addis Valley, West Virginia.   |      |
| FIG. 12. <i>Agelacrinites southworthi</i> , new species.....   | 16   |
| The holotype, $\times 4$ , a specimen perfect in all parts except the anal region.   |      |
| Hamilton (Arkona beds, 20 to 30 feet below the Encrinal limestone): Marsh's Mills, Arkona, Ontario.  |      |
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| A complete example, $\times 4$ , from the original locality exhibiting normal number and direction of ambulacra for the genus.   |      |
| Kinderhook (Legrand formation): Legrand, Iowa.   |      |



## PLATE 5

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- FIG. 1. *Isorophus trentonensis*, new species..... 17  
 A complete example,  $\times 4$ , attached to a brachiopod, exhibiting the short, broad, slightly curved arms and the many plates of large oral area.  
 Trenton (upper part of Deltoidea zone): Trenton Falls, New York.
- FIGS. 2, 3. *Isorophus (Agelacrinus) warrenensis* (James)..... 19  
 (See also pl. 6, fig. 11.)  
 2. A specimen,  $\times 3$ , from the original lot but better preserved than the type. The broad oral area of many plates and the stout, short, curved arms and large overlapping interambulacral plates are characteristic.  
 Richmond (probably basal Arnheim): Oregonia, Ohio.  
 3. Another specimen,  $\times 3$ , attached to a brachiopod, with the ambulacra more clearly defined.  
 Richmond (Waynesville): Clarksville, Ohio.
- FIG. 4. *Cincinnati discus (Hemicystites) carnensis* (Foerste)..... 5  
 One of the type specimens,  $\times 4$ , a slightly worn individual.  
 Trenton (*Strophomena vicina* zone): Carntown, Kentucky.
- FIGS. 5-7. *Hemicystites richmondensis*, new species..... 13  
 5. A small example,  $\times 4$ , slightly abraded, attached to a brachiopod.  
 6. A larger, better-preserved specimen attached to a *Rafinesquina*,  $\times 4$ . The short, broad arms, practically straight, characterize the species.  
 7. Another small example,  $\times 4$ , with plate structure well preserved.  
 Richmond: Warren County, Ohio (5) and Versailles, Indiana (6) (Waynesville); Adams County, Ohio (7) (Whitewater).
- FIGS. 8, 9. *Isorophus (Agelacrinus) holbrooki* (James)..... 18  
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 9. Lateral view of same,  $\times 3$ , showing the plate detail of the anal area and the adjacent ambulacra.  
 Richmond (Lower Arnheim): Morrow, Ohio.
- FIG. 10. *Hemicystites (Agelacrinites) rectiradiatus* (Shideler)..... 12, 14  
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 Richmond (Lower Whitewater): Olive Branch, Harshville, Ohio.
- FIG. 11. *Isorophus (Agelacrinus) cincinnatiensis* (Roemer)..... 17  
 Roemer's original view of the type, reversed, slightly enlarged.  
 Cincinnati (Maysville-Bellevue): Cincinnati, Ohio.

- PAGE
- FIG. 12. *Cincinnatidiscus turgidus*, new species..... 6  
 The holotype,  $\times 4$ , exhibiting the short swollen ambulacra.  
 Richmond (Whitewater): Oxford, Ohio.

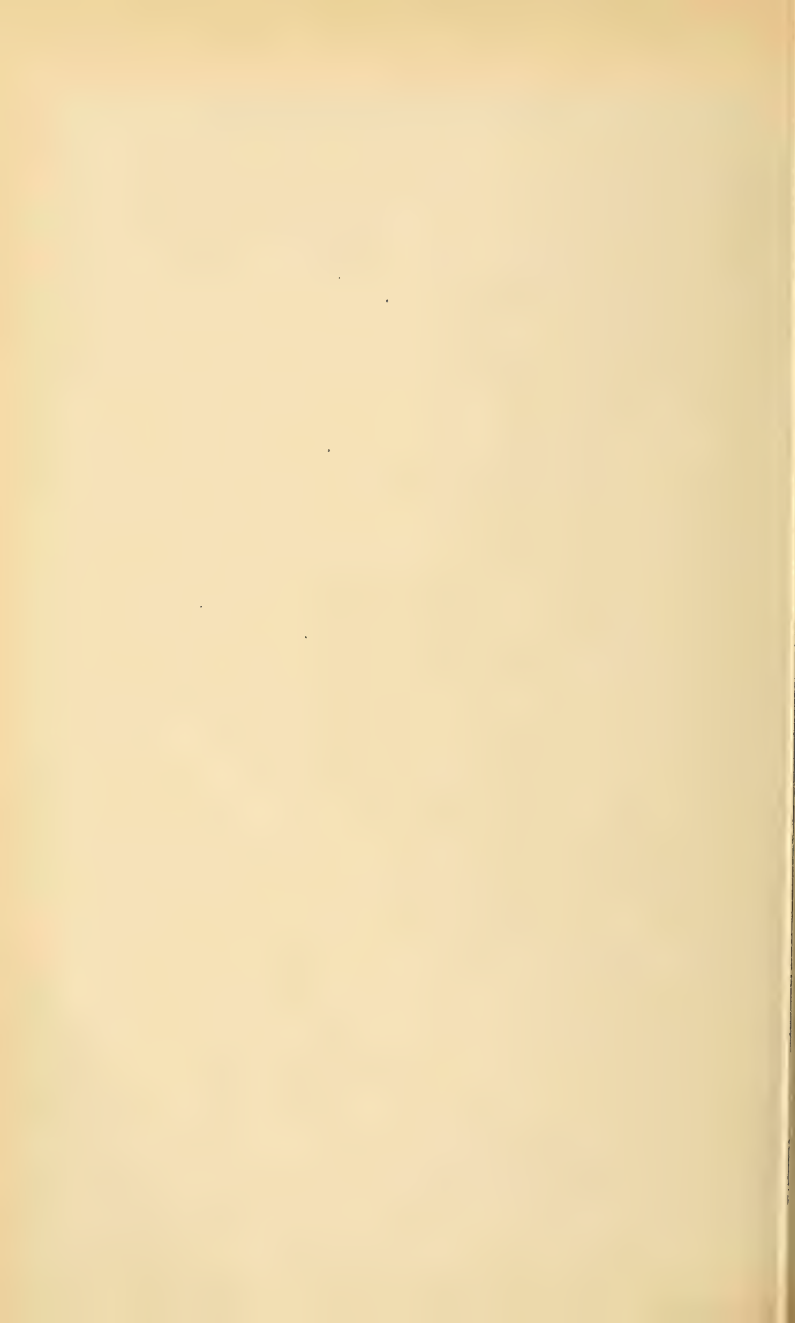
## PLATE 6

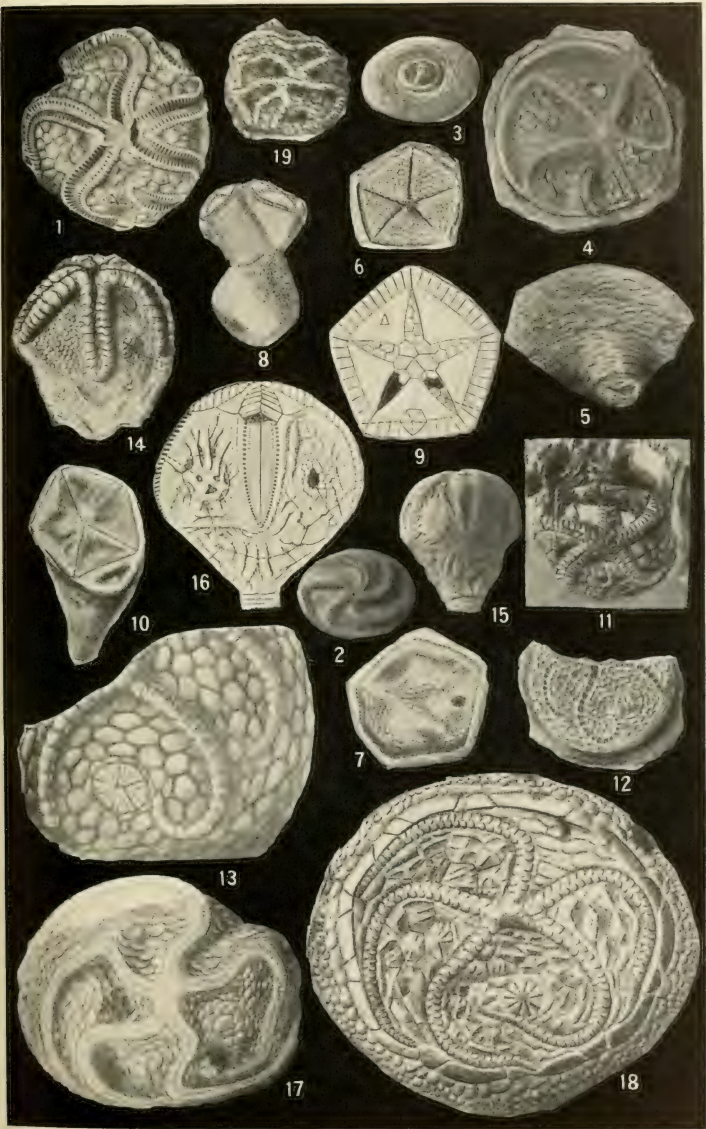
- FIGS. 1, 2. *Isorophus (Agelacrinus) austini* (Foerste)..... 17  
 (See also pl. 2, fig. 9.)  
 1. One of a group of specimens attached to a limestone fragment,  
 $\times 4$ . The ambulacra are partially covered by the marginal  
 rows of plates. Richmond (basal Saluda): Fallen Timbers  
 Creek, Versailles, Indiana.  
 2. Under side of oral surface,  $\times 4$ , showing the ambulacral  
 floor plates arranged in a single row.  
 Richmond (Upper Whitewater): Dodges Creek, Oxford, Ohio.
- FIGS. 3, 4. *Isorophus germanus*, new species..... 18  
 3. The holotype, a fairly well preserved specimen,  $\times 2$ , attached  
 to a brachiopod. The fewer rows of interambulacral plates  
 distinguish it from *I. holbrooki*.  
 4. Another entire example,  $\times 2$ , although slightly worn.  
 Waynesville (Clarksville): Morrow (fig. 3) and Oxford, Ohio.
- FIGS. 5, 6. *Carneyella ulrichi*, new species (Bassler and Shideler)..... 8  
 5. The type example,  $\times 2$ , a somewhat crushed specimen attached  
 to a *Hebertella*.  
 6. View of surface, enlarged, showing ornamentation of oral,  
 ambulacral and interambulacral plates.  
 Cincinnati (Maysville-Bellevue): Railroad cut, south of Mays-  
 ville, Kentucky.
- FIGS. 7, 8. *Carneyella foerstei*, new species (Bassler and Shideler)..... 8  
 7. The holotype,  $\times 2$ , a slightly crushed example attached to a  
*Rafinesquina*.  
 8. Surface ornament, enlarged, exhibiting the elongate nodes of  
 the ambulacral plates.  
 Richmond (Arnheim-*Glyptocrinus* zone): Russellville, Ohio.
- FIG. 9. *Isorophus shideleri*, new species..... 19  
 The complete, although slightly damaged type specimen,  $\times 3$ ,  
 with the characteristic very narrow, long, much recurved  
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 Richmond (Elkhorn): West of Hamburg, Indiana.
- FIG. 10. *Isorophus kentuckyensis*, new species..... 18  
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 layer.  
 Trenton (Woodburn-Greendale contact): Lair Station, Kentucky.
- FIG. 11. *Isorophus warrenensis* (James)..... 19  
 (See also pl. 5, fig. 2, 3.)  
 Photograph,  $\times 2$ , of a specimen probably belonging to this species,  
 showing jumbled condition of plates.  
 Richmond (basal Arnheim): Mouth of Second Creek of Todds  
 Fork, Warren County, Ohio.

## PLATE 7

- |  | PAGE   |
|--|--------|
| FIG. 1. <i>Hemicystites devonicus</i> , new species.....   | 14     |
| The holotype, $\times 4$ , incrusting a <i>Chonetes</i> , exhibiting the short, quickly tapering ambulacra.                            |        |
| Devonian (Long Lake beds of Presque Isle formation): Quarry, Alpena Portland Cement Co., Alpena County, Michigan.                      |        |
| FIG. 2. <i>Hemicystites (Agelacrinites) latiusculus</i> (Barrande).....  | 11     |
| Well-preserved example, $\times 2$ .   |        |
| Ordovician (D4): Zahorzan, Bohemia.  |        |
| FIGS. 3, 4. <i>Hemicystites (Agelacrinites) bohemicus</i> (Barrande).....  | 11     |
| A large distorted specimen and a small, more perfect individual, $\times 1$ .  |        |
| Ordovician (D2): Mount Drabow, Bohemia.  |        |
| FIG. 5. <i>Hemicystites (Agelacrinites) confertus</i> (Barrande).....  | 11     |
| Theca, $\times 1.6$ , with marginal plates little developed.   |        |
| Ordovician (D2): Mount Drabow, Bohemia.  |        |
| FIG. 6. <i>Hemicystites (Agelacrinites) simplex</i> (Barrande).....  | 11     |
| A species similar to the preceding but with well-developed marginal rows, $\times 2$ .   |        |
| Ordovician (D4): Zahorzan, Bohemia.  |        |
| FIG. 7. <i>Lepidodiscus milleri</i> Sharman and Newton.....  | 20     |
| Specimen, $\times 3$ , showing the generic characters clearly.   |        |
| Subcarboniferous: Waterhead, Cumberland, England.  |        |
| FIG. 8. <i>Lepidodiscus (Agelacrinites) buttsi</i> (Clarke).....   | 20     |
| Type specimen, $\times 1.3$ , with broad marginal area.  |        |
| Mississippian (between Wolf Creek conglomerate and Mount Hermon sandstone): Cattaraugus County, New York.                              |        |
| FIG. 9. <i>Agelacrinites (Agelacrinus) blairi</i> (Miller).....  | 16     |
| Photograph of the holotype, $\times 4$ , attached to arms of a batocrinid.   |        |
| Mississippian (Warsaw): Boonville, Missouri.   |        |
| FIG. 10. <i>Agelacrinites hanoveri</i> Thomas.....   | 16     |
| One of the types, $\times 4$ , a small individual with broad marginal rim.   |        |
| Devonian (Shell Rock): Mason City, Iowa.   |        |
| FIG. 11. <i>Discocystis (Agelacrinites) kaskaskiensis</i> (Hall).....  | 21     |
| (See also pl. 1, figs. 4, 5; pl. 3, figs. 4-6.)  |        |
| Basal view of theca, $\times 2$ , showing central opening and many rows of closely packed marginal plates.                             |        |
| Chester (Glen Dean): Sloans Valley, Kentucky.  |        |
| FIG. 12. <i>Isorophusella (Lebetodiscus) incondita</i> (Raymond).....  | 19, 20 |
| A specimen from the type slab, $\times 4$ , showing slightly curved rays and broad oral area.  |        |
| Trenton (Cystid bed): Ottawa, Ontario.   |        |
| FIG. 13. <i>Foerstediscus splendens</i> , new species.....   | 10     |
| Holotype, $\times 4$ , illustrating the dextrally curved rays, mosaic interambulacra, and tubelike anal area of this striking species. |        |
| Black River (Decorah shale, top of <i>Rhinidictya</i> bed); Ford plant, St. Paul, Minnesota.   |        |

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FIG. 14. <i>Xenocystites carteri</i> , new genus and species.....	3
The type specimen, $\times 1.6$ , half of a theca showing basal covering plates and the outlines of four ambulacra impressed upon them. Chemung (Gowanda): Cattaraugus Creek, Versailles, New York.	
FIG. 15. <i>Carneyella</i> ? ( <i>Lebetodiscus</i> ) <i>platys</i> (Raymond).....	7
Photograph of the type specimen, $\times 4$ . Middle Trenton, Ottawa, Canada.	





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(For explanation, see pages 25, 29.)





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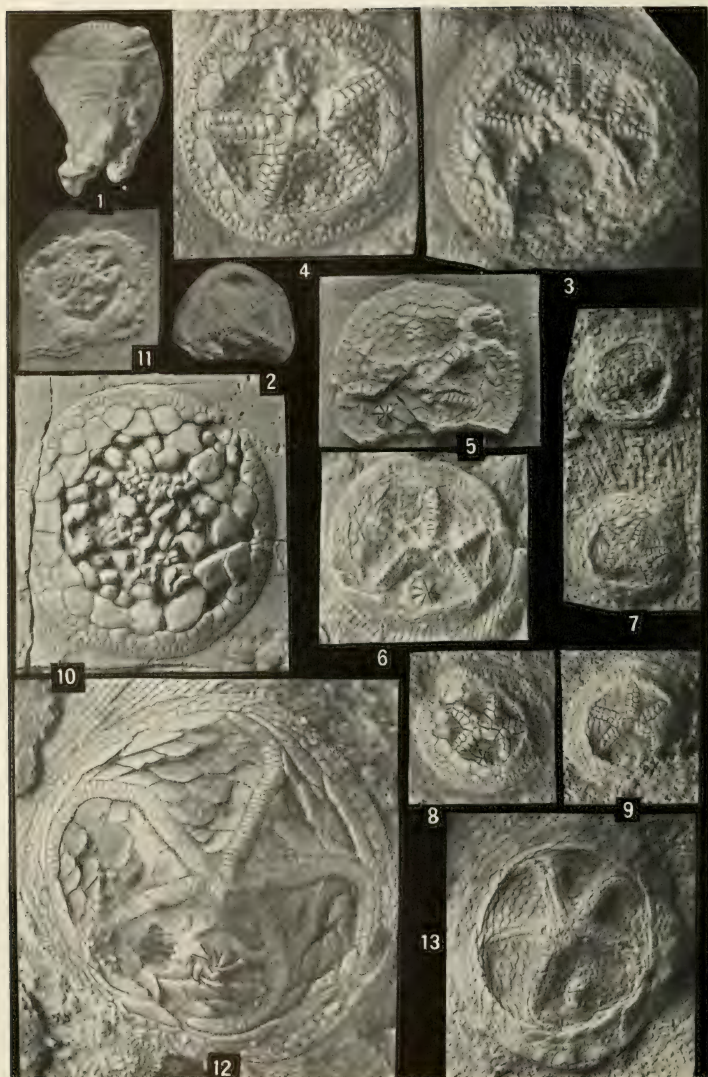
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(For explanation, see pages 27, 28.)



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(For explanation, see pages 28, 29.)



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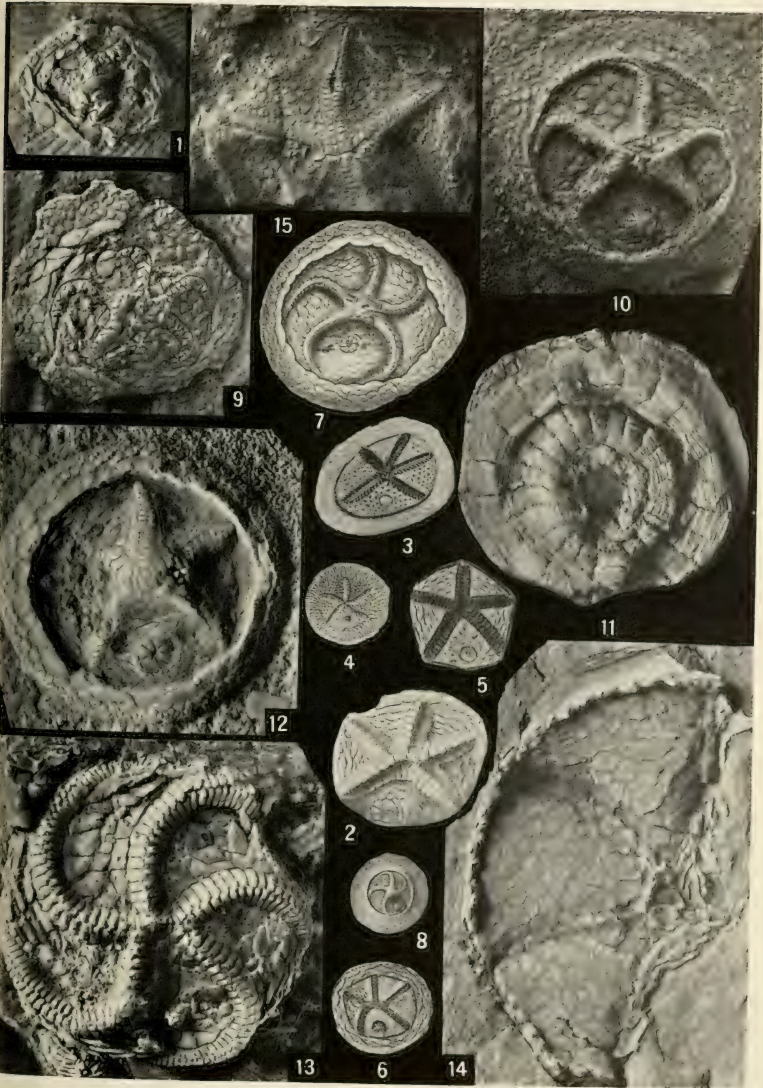
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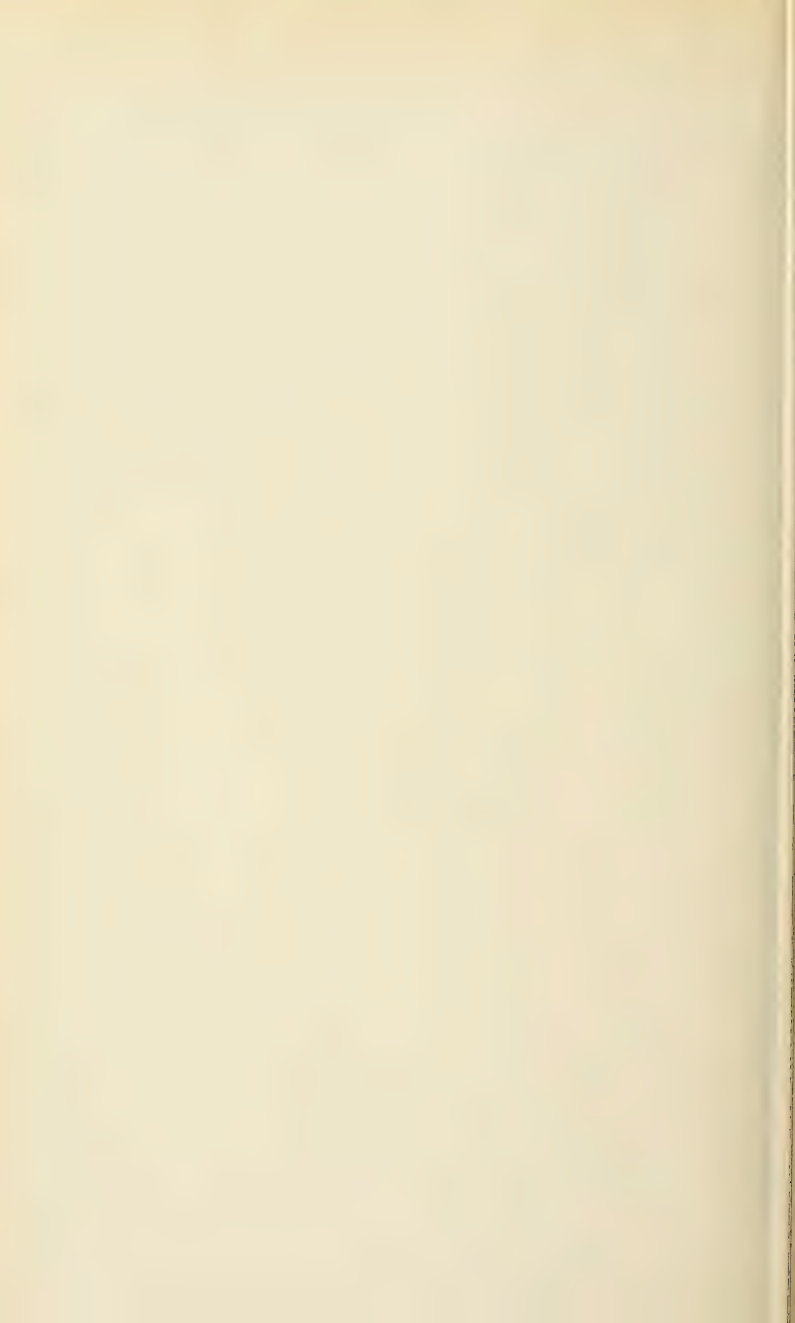
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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95 NUMBER 7

# THE GOLD-BANDED SKIPPER (RHABDOIDES CELLUS)

(WITH EIGHT PLATES)

BY

AUSTIN H. CLARK

U. S. National Museum

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EARLY STAGES OF RHABDOIDES CELLUS

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(WITH EIGHT PLATES)

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## PREFACE

Early in the spring of 1934 while walking through the woods east of Great Falls, Md., Mrs. Leila F. Clark and I came upon a small glade at the base of a rather steep hill where a small stream broadened into a marshy spot. The abundance here of trailing arbutus (*Epigaea*

*repens*) and of hepatica (*Hepatica americana*) indicated that this region had, at least for the most part, escaped the numerous fires that have ravaged these woods in the past, and suggested that it might offer something of interest in its fauna and flora.

Revisiting the locality on May 30, we were somewhat surprised to find a gold-banded skipper (*Rhabdoides cellus*), a rare butterfly in this region. On June 3 we caught seven. Evidently the butterfly was common enough here to make the working out of its life history a comparatively simple task. So we undertook an intensive study of the insect and were fortunate enough to secure abundant material of all stages.

As no general account of this interesting butterfly has heretofore been published, it has seemed to us worth while to preface the record of our personal observations with the references to previous notices of the species, a list of the localities from which it is known, and a brief history. This appeared to us especially desirable for the reason that the gold-banded skipper is an excellent example of a butterfly with its normal habitat in the highlands of Mexico and Southern Arizona and a secondary habitat, in which it appears to have an uncertain and precarious foothold, in the more or less mountainous country near the eastern seaboard from southern New York to Florida.

In our study of this species we have been greatly aided by Capt. N. D. Riley, Keeper of Entomology in the British Museum (Natural History), who was so very kind as to send us a list of all the specimens from north of Mexico in the collections under his care; by Dr. William J. Gerhard, who generously sent us a list of the specimens in the Strecker and Snyder collections in the Field Museum of Natural History, Chicago; by Ernest L. Bell, of Flushing, Long Island, N. Y., who was so good as to supply us with a list of the specimens in his collection, and also of those that he had given to the American Museum of Natural History, New York; by Edward S. Thomas of the Ohio State Museum, at Columbus, who most courteously sent us the records (hitherto unpublished) from Ohio; by Prof. Franklin Sherman, Head of the Department of Entomology and Zoology at the Clemson Agricultural College, who kindly sent us the records (unpublished) from South Carolina; by Dr. Hugo Kahl, of the Carnegie Museum, at Pittsburgh, Pa., who courteously permitted us to examine the specimens in the William H. Edwards collection; and by Prof. Ellison A. Smyth, Jr., formerly Head of the Department of Biology at the Virginia Polytechnic Institute at Blacksburg, Va. (now retired and living at Salem, Va.), who was so very good as to send us his notes on this species.



We are under special obligations to the late Foster H. Benjamin and to Dr. William Schaus, of the Bureau of Entomology and Plant Quarantine, who permitted us to study the material under their care, and in addition aided us in every possible way.

To Dr. John A. Comstock, Associate Director of the Los Angeles Museum, and to Commander Charles M. Dammers, of Riverside, Calif., we are indebted for their courtesy in answering our inquiries regarding the possible occurrence of this butterfly in California.

During a visit to St. Louis Dr. Edwin P. Meiners told us of a specimen that had been captured in that State, and later was so very kind as to send us complete information in regard to it.

### RHABDOIDES CELLUS (Boisduval and Le Conte)

Plates 1-3, figs. 1-16

*Eudamus cellus* BOISDUVAL and LE CONTE, Histoire générale et iconographie des lépidoptères et des chenilles de l'Amérique septentrionale, pl. 73, Paris, 1833 (colored figures of both surfaces of imago, pupa, and larva on leaf of *Breweria aquatica*).—HERRICH-SCHÄFFER, Corresp.-Blatt zool.-mineralog. Ver. Regensburg, 19 Jahrg., no. 12, p. 180, no. 73, 1865 (diagnosis).—SCUDDER, A systematic revision of some of the American butterflies, with brief notes on those known to occur in Essex County, Mass., p. 62, 1872 (has not been able to examine or determine this species); also in Rep. Peabody Acad. Sci., 1871, p. 83, 1872 (same).—W. H. EDWARDS, Report upon geographical and geological explorations and surveys west of the One Hundredth Meridian, in charge of First Lt. Geo. M. Wheeler, vol. 5, Zoology, chap. 8, p. 794, 1875 (in list of Lepidoptera collected in 1871-1874 in Calif., Nev., Utah, Colo., N. Mex., and Ariz.).—W. H. EDWARDS, Catalogue of the diurnal Lepidoptera of America north of Mexico, Trans. Amer. Ent. Soc., vol. 6, p. 58, no. 495, 1877 (Southern States; W. Va., Ky.; Ariz.).—SPEYER, in Lintner, Systematic arrangement of the European and some American Hesperidae, Ent. Contr., no. 4, 12, p. 72, 1878 (listed).—STRECKER, Butterflies and moths of North America, p. 162, no. 341, Reading, Pa., 1878 (Va. southward to the Gulf of Mexico).—GLOVER, in unpublished notes, pl. B, fig. 25 (larva and pupa; from Boisduval and Le Conte); pl. F, fig. 13 (imago, both surfaces; from the same).—PUBLICATION COMMITTEE, Brooklyn Entomological Society, Check list of North American Macro-Lepidoptera, p. 5, no. 566, Brooklyn, N. Y., 1881; also published in Bull. Brooklyn Ent. Soc., vol. 4, p. 5, no. 566, October 1881 (listed).—PLÖTZ, Ent. Zeit., Stettin, Jahrg. 43, nos. 1-3, p. 95, Januar-März 1882 (synonym of *festus* Hübner).—W. H. EDWARDS, Papilio, vol. 3, no. 1, p. 10, January 1883 (Ariz.; vicinity of Fort Grant, Cochise Co., or on Graham Mountain).—W. H. EDWARDS, Revised catalogue of the diurnal Lepidoptera of America north of Mexico, 1884; also published in Trans. Amer. Ent. Soc., vol. 11, p. 320, November 1884 (listed; *festus* Hübner a synonym; W. Va. to Gulf of Mexico; Tex.; Ariz.).—W. H. EDWARDS, List of species of the diurnal Lepidoptera of America north of Mexico, Butterflies of North America,

vol. 2, no. 596, 1884 (listed).—FRENCH, Butterflies of the eastern United States, pp. 371-372, no. 194, 1886 (description; W. Va. to the Gulf of Mexico; Tex.; Ariz.).—W. H. EDWARDS, Butterflies of North America, 3d ser., pt. 5, *Debis* 1, 5th page of text, 1888 (occurrence near Coalburgh, W. Va.).—HENRY EDWARDS, U. S. Nat. Mus. Bull. 35, p. 37, 1889 (early stages; from Boisduval and Le Conte).—SMITH, Catalogue of insects found in New Jersey, in Cook, Final Rep. State Geologist, Geol. Surv. New Jersey, vol. 2, pt. 2, p. 279, 1890 (taken rarely by the Newark collectors).—SKINNER, Ent. News, vol. 2, no. 1, suppl. p. iv, January 1891 (listed in exchange list of butterflies of America north of Mexico).—SKINNER, in Smith, List of Lepidoptera of Boreal America, p. 17, no. 624, Philadelphia, 1891 (listed).—MAYNARD, Manual of North American Butterflies, p. 209, no. 596, Boston, 1891 ("yellow-banded brown-wing"; description; W. Va. to the Gulf of Mexico; Tex.; Ariz.).—BEUTENMÜLLER, Bull. Amer. Mus. Nat. Hist., vol. 5, p. 304, 1893 (description; description of larva and pupa, abridged from Scudder, after Abbot's figures; food plants Convolvulaceae; vicinity of Newark, N. J., after Smith); pl. 5, fig. 18.—WHITE, Ent. News, vol. 5, no. 6, p. 175, June 1894 (Prospect Park, Brooklyn, N. Y.; 1893).—SMYTH, Ent. News, vol. 6, no. 8, p. 244, October 1895 (Montgomery Co., Va.).—OSBURN, Ent. News, vol. 6, no. 9, p. 283, November 1895 (Nashville, Tenn.; rare; one specimen, August; food plant unknown).—FRENCH, Butterflies of the eastern United States, p. 371, no. 194, 1896 (from 1886 edition).—SKINNER, A synonymic catalogue of the North American Rhopalocera, p. 97, no. 629, Philadelphia, Dec. 15, 1898 (W. Va. to Gulf of Mexico; Tex.; Ariz.; Mexico).—SMITH, Insects of New Jersey; suppl. 27th Ann. Rep. State Board of Agriculture, 1899, p. 383, 1900 (taken rarely near Newark; larvae on Convolvulaceae).—BARNES, Ent. News, vol. 11, no. 1, p. 332, 1900 (very common in the Huachuca Mountains, Ariz.); the same paper reset and repaged, entitled Notes on North American diurnals with some additions and corrections to Dr. Skinner's catalogue, p. 5, 1900 (very common in the Huachuca Mountains, Ariz.).—BEUTENMÜLLER, The butterflies of the vicinity of New York City; Guide Leaflet No. 7, Suppl. Amer. Mus. Journ., vol. 2, no. 5, p. 50, no. 91, May 1902 (gold-banded hesperid; exceedingly rare in this neighborhood, but more common in the Southern States and Mexico); figure, p. 50.—SMITH, Check list of the Lepidoptera of Boreal America, p. 13, no. 672, June 1903 (listed).—KUNZE, Ent. News, vol. 15, p. 240, 1904 (Huachuca Mountains; on flowers of *Rudbeckia*).—SKINNER, Synonymic catalogue of the North American Rhopalocera, suppl. no. 1, p. 33, 1905 (listed).—WRIGHT, Butterflies of the West Coast of the United States, p. 68, San Francisco, 1905 (South Atlantic States).—BEUTENMÜLLER, A manual of American and European butterflies and moths, reproduced in natural colors, with their common and scientific names, pl. 7, nos. 47, 47a, New York and London, 1906.—BRIMLEY and SHERMAN, Ent. News, vol. 18, no. 3, p. 100, March 1907 (Tryon, N. C., May, June, July).—LINDSEY, Ann. Ent. Soc. Amer., vol. 18, no. 1, p. 100, March 1925 (haplotype of *Rhabdoides*).—SMITH, Report on the insects of New Jersey, Ann. Rep. New Jersey State Mus., p. 424, Trenton, 1910 (taken rarely at Newark; larva on *Convolvulus*).—FRENCH, Butterflies of the eastern United States, 4th ed., p. 371, no. 194, 1914 (from previous editions).

- (*Papilio gentilis*, *Astycus celebris*) *Cecrops festus* GEYER, in Hübner, Zuträge zur Sammlung exotischer Schmetterlinge, Fünftes Hundert, p. 27, figs. 907, 908, 1837 (description; no locality).
- Hesperia cellus* DOUBLEDAY and WESTWOOD, Genera of diurnal Lepidoptera, vol. 2, p. 526, no. 9, 1852 (United States).—MORRIS, Smithsonian Misc. Coll., vol. 3, p. 14, May 1860 (listed); vol. 4, p. 105, February 1862 (description; United States).
- Hesperia festus* DOUBLEDAY and WESTWOOD, Genera of diurnal Lepidoptera, vol. 2, p. 526, no. 10, 1852 (? locality).
- Goniloba cellus* WEIDEMEYER, Catalogue of North American butterflies, p. 38, Philadelphia, 1864 (United States); reprinted in Proc. Ent. Soc. Philadelphia, vol. 2, p. 538, March 1864 (references; United States).
- Eudamus festus* HERRICH-SCHÄFFER, Corresp.-Blatt zool.-mineralog. Ver. Regensburg, 23 Jahrg., no. 12, p. 186, no. 3, 1869 (in key).—PLÖTZ, Ent. Zeit., Stettin, Jahrg. 43, nos. 1-3, p. 95, no. 62, Januar-März, 1882 (references; short description; *cellus* included as a synonym).
- Spathilepia cellus* BUTLER, Entomologist's Monthly Mag., vol. 7, p. 57, 1870 (listed as belonging to the new genus *Spathilepia*).—KIRBY, Synonymic catalogue of diurnal Lepidoptera, p. 578, no. 5, London, 1871 (listed).—W. H. EDWARDS, Synopsis of North American butterflies, in Butterflies of North America, vol. 1, p. 39, 1872 (Southern States; W. Va.).—GERHARD, Systematische Verzeichniss der Macro-Lepidopteren von Nord-America, p. 27, no. 468, Leipzig, 1878 (listed; Union).
- Thymele festus* KIRBY, Synonymic catalogue of diurnal Lepidoptera, p. 571, no. 35, London, 1871 (listed).
- Rhabdoides cellus* SCUDDER, Butterflies of the eastern United States and Canada, vol. 3, p. 1855, 1889 (detailed description of the imago; descriptions of the larva and pupa from Abbot's figures; Ga. to Ariz., and as far north as W. Va. and Ky.; Mexico; Putta, about 150 miles from Oaxaca, on the Pacific slope; Tallahassee, Fla., Apr. 17; notes).—E. Y. WATSON, Proc. Zool. Soc. London, p. 34, January 17, 1893 (listed).—SCUDDER, Brief guide to the commoner butterflies of the northern United States and Canada, p. 166, New York, 1893 (a southern type found at least as far north as W. Va. and Ky.).—GODMAN and SALVIN, Biologia centrali-Americana, Insecta, Lepidoptera-Rhopalocera, vol. 2 (text), p. 331, 1894 (North America; Southern States; Ariz.; Mexico; Milpas, in Durango; Cuernavaca, June; Xucumanatlan; Omilteme; Mexico City; Pinal, near Puebla; Oaxaca; Putla; notes); vol. 3 (plates), pl. 80, fig. 8, 1894 (male genitalia).—DYAR, U. S. Nat. Mus. Bull. 52, p. 57, no. 586, 1902 (South Atlantic States; Ariz.; Mex.).—MABILLE, Genera Insectorum, publiés par P. Wytsman, 17<sup>a</sup> fasc., Lepidoptera Rhopalocera, Fam. Hesperidae, p. 29, Bruxelles, 1903 (listed; North America).—J. H. and A. B. COMSTOCK, How to know the butterflies, p. 294, New York, May 1904 (short description; W. Va. to the Gulf of Mexico); pl. 44, fig. 2 (colored).—DYAR, Journ. New York Ent. Soc., vol. 13, p. 114, September 1905 (occurs in Arizona).—FORBES, Field tables of Lepidoptera, 1906, p. 16, Worcester, Mass. (markings and size).—MABILLE and BOULLET, Ann. Sci. Nat., Zool., 87<sup>e</sup> ann., 9<sup>e</sup> sér., vol. 16, nos. 1-4, p. 128, 1912 (description); p. 129 (synonymy; record of specimens examined).—BARNES and McDUNNOUGH, Check list of the Lepidoptera of Boreal America, p. 18, Decatur, Ill., February 1917 (listed).—GROSSBECK,

- Bull. Amer. Mus. Nat. Hist., vol. 37, art. 1, p. 27, 1917 (Tallahassee, Fla., Apr. 17; Biscayne Bay, Fla.).—DRAUDT, in Seitz, Macrolepidoptera of the world, vol. 5, p. 871, 1922 (diagnosis; widely distributed in North and Central America); p. 1048 (*pseudocellus*, treated on p. 871 as a form of *cellus*, separated as a distinct species); pl. 169, rows a and b.—FORBES, in Leonard, List of the insects of New York, Mem. 101, Cornell Univ., Agr. Exp. Stat., p. 670, August 1926, issued January 1928 (Brooklyn, N. Y.; presumably a stray).—HOLLAND, Butterfly book, revised ed., p. 338, pl. 45, fig. 12, 1931 (the Virginias southward and westward to Ariz. and Mexico; common in the Carolinas; Mexican specimens are larger and the light band is narrower).—A. H. CLARK, Science, n. s., vol. 80, no. 2068, pp. 163-164, Aug. 17, 1934 (brief account of the life history).
- Achalarus cellus* HOLLAND, Butterfly book, p. 326 (the Virginias southward and westward to Ariz. and Mexico; common in the Carolinas); pl. 45, fig. 12; reprinted, 1910.—COOLIDGE and CLEMENCE, Ent. News, vol. 22, no. 1, p. 4, January 1911 (compared with *A. pseudocellus*, spec. nov.).—HOLLAND, The butterfly guide, p. 202, New York, 1915 (Virginias southward to Ariz. and Mexico); pl. 132, p. 202, fig. 2 (colored); reprinted, 1923.
- Achalarus cellus* GIRAULT, Ent. News, vol. 11, p. 439, 1900 (abundant in Anne Arundel Co., Md.).
- Cecrops festus* KIRBY, Zuträge zur Sammlung exotischer Schmetterlinge . . . von Jacob Hübner und Carl Geyer, new English facsimile edition, p. 24, Brussels, 1908-1912 (Mexico; figure is of a female); p. 92 (distribution, North America).
- Eudamus (Rhabdoides) cellus* SKINNER, Trans. Amer. Ent. Soc., vol. 37, p. 189, 1911 (description of imago, larva, and pupa, the first from French, 1886, the last two from Scudder, 1889; W. Va. to the Gulf of Mexico; Tex.; Ariz.; Mexico; Putta; Colima; Milpos; Cuernavaca; Xucumanatlan; Omilteme; Pinal; Mexico City; Oaxaca; Nashville, Tenn., Aug. 19 (Osborn); Tallahassee, Fla., Apr. 17 (Maynard); Ga., Apr. 25 (Abbot); food plant *Breweria aquatica*; apparently two broods).
- Cecropterus cellus*, LINDSEY, Univ. Iowa Studies, Studies in Nat. Hist., vol. 9, no. 2 (in reality no. 4), 1st ser., no. 43, p. 31, Feb. 15, 1921 (synonymy; Pa., July; Va. and W. Va., May and June; Tex. and Ariz., April and August); fig. 9, a (club of antenna), b (detail of neuration of anal area of secondary), p. 30.—SKINNER and WILLIAMS, Trans. Amer. Ent. Soc., vol. 48, no. 2, p. 120, June 1922 (description of male genitalia); fig. 19, p. 119 (male genitalia; Mount Graham, Ariz.).—BARNES and BENJAMIN, Check list of the diurnal Lepidoptera of Boreal America, San Diego, California, p. 21, 1926 (listed; *festus* Geyer included as a synonym, and *aereofuscus* Gunder as an aberration); republished a few days later in Bull. Southern California Acad. Sci., vol. 25, part 1, p. 21, January-April, 1926 (same).—HARRIS, A list of the butterflies of Georgia, Trans. Georgia Naturalists Club, vol. 1, no. 1, p. 21, January 1931 (Macon, Ga.).—LINDSEY, BELL, and WILLIAMS, Denison Univ. Bull., Journ. Sci. Lab., vol. 26, p. 31, April 1931 (Pa., July; Va. and W. Va., May-August; Tex. and Ariz., April, July-September; synonymy); pl. 1, fig. 10, a, b (from Lindsey, 1922); pl. 5, fig. 2 (male genitalia).—A. H. CLARK, U. S. Nat. Mus. Bull. 157, p. 204, 1932 (D. C., June 25, 1889; Difficult Run, Va., June 23, 1920; Collington, Md., July 30, 1930); pl. 50, figs. 3, 4 (specimen without data).—RICHARDS, Bull.

Brooklyn Ent. Soc., n. s., vol. 26, no. 5, p. 250, December 1931 (River Falls, S. C., August; Calahan Mountain, S. C., June; Macon, Ga.).

*Autochton cellus* H. H. SHEPARD, Lepidopterorum Catalogus editus ab Embrik Strand, pars 47, Hesperidae, Subfamilia Pyrginae I., p. 83, Dec. 4, 1931 (very detailed references; U. S.; Mexico).

*Rhabdoites cellus* A. H. and L. F. CLARK, The Auk, new series, vol. 51, no. 4, October 1934, p. 528 (near Great Falls, Md.; early stages).

*Type locality*.—Jacksonborough, county seat of Scriven County, Ga.

*Type*.—Raised from a full-grown caterpillar found on a leaf of *Breweria aquatica*. The adult emerged on April 25, the caterpillar having pupated 3 weeks previously.

### LOCALITY RECORDS

NEW YORK: Prospect Park, Brooklyn, Long Island, 1893 (H. G. White, 1894; W. T. M. Forbes, 1928, as Brooklyn, L. I.).

NEW JERSEY: Newark (J. B. Smith, 1890; Beutenmüller, 1893).

PENNSYLVANIA: July; no further data (Lindsey, Bell, and Williams, 1931); Lititz, near Lancaster, June 25, July 14, 16, 1892; J. J. Heiserman (3, U.S.N.M.).

MARYLAND: Collington, July 30, 1930 (A. H. Clark, 1932). Opposite Widewater, 1.1 miles southeast of Great Falls (A. H. Clark, 1934, as vicinity of Washington). Anne Arundel County (Girault, 1900).

DISTRICT OF COLUMBIA: Washington, June 25, 1889, Ernest Shoemaker (A. H. Clark, 1932).

VIRGINIA: May-August; no further data (Lindsey, Bell, and Williams, 1931). Great Falls, Fairfax County, June 4 (E. L. Bell collection). Difficult Run, Fairfax County, June 23, 1920, Ernest Shoemaker (A. H. Clark, 1932). Fairfax County, June 24, 1925, F. M. Schott (1, U.S.N.M.). Fairfax County, June 23 (E. L. Bell collection). Buckingham, Buckingham County, June (Amer. Mus. Nat. Hist., from the E. L. Bell collection). Buckingham County, Aug. 16 (E. L. Bell collection). Wingina, Nelson County (Amer. Mus. Nat. Hist., from the E. L. Bell collection). Montgomery County (Smyth, 1895; Skinner, 1911).

WEST VIRGINIA: No further data (W. H. Edwards, 1872; French, 1886; Scudder, 1889). Same (1, Strecker coll., Field Mus.). May-August; no further data (Lindsey, Bell, and Williams, 1931). Charleston, May 18, 22, 30, 1900 (4, U.S.N.M.). Kanawha County (5, W. H. Edwards coll., Carnegie Mus.). Coalburgh, W. H. Edwards, July 25, 1886 (1, W. H. Edwards coll., Carnegie Mus.).

OHIO: Hocking and Jackson Counties, in the southeastern part of the State, 1934 (Edward S. Thomas, *in litt.*).

KENTUCKY: No further data (W. H. Edwards, 1877; Scudder, 1889).

TENNESSEE: Nashville, August (Osburn, 1895; Skinner, 1911, with the date Aug. 19).

NORTH CAROLINA: No further data; H. K. Morrison (1 male, British Mus.). Tryon, Polk County, in the southwestern part of the State, May, June, July (Brimley and Sherman, 1907).

SOUTH CAROLINA: River Falls, in the mountains in the western part of the State, 1,500 to 2,700 feet; Henry K. Townes, Jr., August (Richards, 1931). Calahan Mountain; Henry K. Townes, Jr., June (Richards, 1931). Greenville



County, in mountains, June to August; Henry K. Townes, Jr. (Franklin Sherman, *in litt.*). Rocky Bottom, Pickens County, June 1, 1933, June 21, 1932, Aug. 9-12, 1927, Aug. 31, 1930; Franklin Sherman (Franklin Sherman, *in litt.*).

GEORGIA: No further data; Henry Edwards (1 male, British Mus.). Near Jacksonborough, a town formerly existing about 8 miles north of Sylvania, Screven County; John Abbot, Apr. 25 (Boisduval and Le Conte, without locality, 1833; Scudder, as Georgia, 1889; Skinner, as Georgia, 1911). Macon, Bibb County, in the central part of the State; Strohecker (Harris, 1931; Richards, 1931).

FLORIDA: No further data (3 males, of which 2 are from H. Strecker, British Mus.). Same (2, Strecker coll., Field Mus.). Same (1, W. H. Edwards coll., Carnegie Mus.). Tallahassee, April 17, C. J. Maynard (Scudder, 1889; Skinner, 1911). Tallahassee; Albert Koebele (1, U.S.N.M.). Biscayne Bay; Annie Trumbull Slosson (Grossbeck, 1917).

MISSOURI: Seventy-six, Perry County; Herman Schwarz, July 20, 1919 (Edwin P. Meiners, *in litt.*).

TEXAS: No further data (French, 1886; Skinner, 1911). Same (1 female, British Mus.). April, July-September; no further data (Lindsey, Bell, and Williams, 1931). Kerrville, Kerr County; H. Lacy (9, U.S.N.M., one dated May 1901). Kerrville, Apr. 10 (E. L. Bell coll.).

ARIZONA: No further data (French, 1886; Scudder, 1889; Godman and Salvin, 1894; Dyar, 1905; Skinner, 1911). Same (3, U.S.N.M.). Same (7 males, 2 females, British Mus.; 4 males, 2 females, H. K. Morrison; 2 males from W. H. Edwards coll.). April, July-September; no further data (Lindsey, Bell, and Williams, 1931). Southern Arizona; Poling (10, 2 dated September 1900; Snyder coll., Field Mus.). Same (5, U.S.N.M., 2 dated September 1900). White Mountains, in the central eastern part of the State (1, U.S.N.M.). Santa Catalina Mountains (1, U.S.N.M.). Palmerlee, Cochise County (9, U.S.N.M.). Same (Amer. Mus., New York, from the E. L. Bell coll.). Chiricahua Mountains, Cochise County; V. L. Clemence (3 males, British Mus.). Vicinity of Fort Grant, Cochise County, or on Graham Mountain; H. K. Morrison, 1882 (W. H. Edwards, 1883). Mount Graham (Skinner and Williams, 1922). Fort Grant; H. K. Morrison (5 males, 2 females, British Mus.). Cochise County (5 males, British Mus.). Paradise, July (Amer. Mus., New York, from the E. L. Bell coll.). Ramsey Cañon, Huachuca Mountains, Cochise County; 5,000 to 7,000 feet; June-July (Coolidge and Clemence, 1911). Huachuca Mountains, July 16-23, 24-30, Aug. 16-23, 24-30 (Barnes, 1900; 7, U.S.N.M.). Huachuca Mountains (Kunze, 1904). Tucson, Pima County, July 1-15 (E. L. Bell coll.). Baboquivari Mountains, Pima County, July 15, 1924 (Gunder, 1925). Same locality, August (2, U.S.N.M.). Arizona mountains (4, W. H. Edwards coll., Carnegie Mus.).

NORTH AMERICA: No further data (1 female, Boisduval coll., British Mus.). Same (Mabille and Boullet, 1912; they record 1 male in the Paris Mus. from the Boisduval collection; 2 females in the Mabille collection; and in addition 2 males and females—6 in all).

MEXICO: No further data (Geyer, 1837, according to Kirby, 1908-1912). Same (Scudder, 1889; Skinner, 1911). Milpas, State of Durango, Forrer (Godman and Salvin, 1894; Skinner, 1911). Guadalajara, State of Jalisco (1, U.S.N.M.). Jalisco, July 15 (E. L. Bell coll.). Xucumanatlan, H. H. Smith (Godman and Salvin, 1894; Skinner, 1911). Omilteme, H. H. Smith (Godman and Salvin,

1894; Skinner, 1911). Colima, State of Colima (Skinner, 1911). Ciudad Mexico, Distrito Federal, Schumann (Godman and Salvin, 1894; Skinner, 1911). Same locality, August, R. Müller (1, U.S.N.M.). Mount Popocatepetl, 8,000 feet, June 1906 (1, U.S.N.M.). Cuernavaca, State of Morelos, June, H. H. Smith (Godman and Salvin, 1894; Skinner, 1911). Same locality, June 1906 (2, U.S.N.M.). Same locality, July 1906 (1, U.S.N.M.). Pinal, near Puebla, State of Puebla, F. D. Godman (Godman and Salvin, 1894; Skinner, 1911). Jalapa, State of Vera Cruz (2, U.S.N.M.; 2 Strecker coll., Field Mus.). Orizaba, State of Vera Cruz (Draudt, 1922). Balsas, northwestern Guerrero (E. L. Bell coll.). Oaxaca, State of Oaxaca, Fenochio (Godman and Salvin, 1894; Skinner, 1911). Same locality (1, U.S.N.M.). Putta, or Putla, about 150 miles from Oaxaca, on the Pacific slope (Scudder, 1889; Godman and Salvin, 1894; Skinner, 1911).

GUATEMALA: Volcan Santa Maria, William Schaus and John Barnes, June (1, U.S.N.M.).

No LOCALITY: Sept. 16, 1923 (1, U.S.N.M.). Collection of C. V. Riley (2, U.S.N.M.). Collection of Charles Oberthur (1, U.S.N.M.). Collection of Kate B. Preston (1, U.S.N.M.). Collection of W. H. Edwards (2, one of which is the original of the colored figures published by Holland; Carnegie Mus.). No data (5, U.S.N.M.).

The records from Anne Arundel County, Md., and Biscayne Bay, Fla., are interesting in being from regions of a type not usually inhabited by this butterfly, and we would like to see them confirmed. We confess to a certain amount of doubt in regard to them.

Capt. N. D. Riley wrote us that there is in the British Museum a specimen from Lord Walsingham's collection labeled "California." Lord Walsingham himself collected only in northern California, mainly in Colusa, Shasta, and Siskiyou Counties in July and August, 1871. He was always exceedingly careful regarding the labeling of his material. The specimen was presumably acquired by purchase or otherwise, and was mislabeled before coming into his possession. Dr. John A. Comstock, whose word regarding the occurrence of butterflies in California we consider as final, writes us that this species does not occur in California, and Commander Charles M. Dammers, whose knowledge of Californian butterflies is exhaustive, is equally positive on this point.

#### RANGE AND DISTRIBUTION

According to Forbes, the specimen recorded from Brooklyn by White was presumably a stray individual. In New Jersey it is said to be taken rarely by the Newark collectors, and in Pennsylvania we know it only from Lititz, where it appears to be rare. It has not been found in Delaware, and in Maryland it is known only from Anne Arundel County, where in 1900 it was said to be common; from a single individual recorded from Collington; and from near Great



Falls, where in 1934 and 1935 it was fairly common, though by no means abundant. There is a single record for the District of Columbia.

From Virginia it is known for the most part only through the capture of individuals from a number of widely scattered localities; but Smyth in 1895 said that it is occasionally taken in Montgomery County. The only localities we know in West Virginia are Charleston and Coalburg, in Kanawha County, where it is not common.

In Ohio it was taken for the first time in 1934, in two of the southeastern counties, as Edward S. Thomas has been so kind as to inform us by letter. William H. Edwards gave Kentucky among the localities for this species, but did not say on what grounds, and Osburn speaks of it as rare at Nashville, Tenn., where he took a single specimen.

In North Carolina it is known only from Tryon, and in South Carolina only from Greenville and Pickens Counties in the western part of the State, so we do not understand Dr. W. J. Holland's statement that "It is common in the Carolinas."

In his manuscript notes, quoted by Scudder, Abbot expressly calls it rare in the vicinity of Jacksonborough, Ga., and Harris, who recorded it from Macon, spoke of it as rare. From Florida it is recorded only from Tallahassee and Biscayne Bay. In Missouri a single specimen, almost fresh, was captured at Seventysix.

There are no records of this species from Alabama, Mississippi, or Louisiana, and in Texas it is only known from Kerrville, where it seems to be fairly common.

It is locally common in southern Arizona, and Barnes wrote that it is very common in the Huachuca Mountains near the Mexican border.

It is not known from New Mexico or from California.

In Mexico, according to Godman, it has a wide range in the highlands, occurring at an elevation of 6,000 feet in the Sierra Madre of Durango, as high as 8,000 feet in the Sierra Madre del Sur, and at similar altitudes in other parts of Mexico. It also occurs at Cuernavaca, where H. H. Smith found it in July.

The southernmost locality from which it is known is the Volcan Santa Maria in Guatemala, where a specimen now in the United States National Museum was captured by William Schaus and John Barnes in June.

The known range of this butterfly—from New York to Florida, about Kerrville, Tex., and from southern Arizona southward to Guatemala—is curiously discontinuous.

Furthermore, though it is generally common in Mexico and in the mountains of southern Arizona, in the eastern States, though widely distributed, it is very local, occurring at widely separated stations almost exclusively in hilly or mountainous regions where it is found in small numbers—indeed from many localities there is only a single record. It is true that its habits are such as to cause it easily to be overlooked, yet if it were anywhere really numerous in the eastern States, or if it were generally distributed, this certainly would be reflected in the records.

Most of the specimens in collections are from Arizona or Mexico. No collection contains a long series of eastern specimens, nor more than a very few eastern examples from any one locality.

The explanation of the distribution of the gold-banded skipper would seem to be that its true habitat is in Mexico and the mountains of southern Arizona, where it is locally a common permanent resident. In the eastern States it is a casual resident of erratic and fortuitous occurrence, maintaining its foothold by virtue of constant new arrivals from the southwest coupled with redistribution from local more or less permanent centers; though constantly present, it cannot properly be regarded as an endemic species in this area.

We believe its status to be parallel to that of *Strymon ontario ontario*, which appears to be frequent about St. Louis, Mo., but farther east and northeast merely an erratic casual visitor.

## THE NAMED VARIETIES OF RHABDOIDES CELLUS

### Var. AEREOFUSCUS Gunder

*Rhabdoides cellus* ab. ♂ *aereofuscus* GUNDER, Ent. News, vol. 36, p. 196, pl. 5 (facing p. 193), fig. 6, 1925 (diagnosis; Baboquivari Mountains, Pima Co., Ariz.; July 15, 1924).

*Cecropterus cellus* ab. *aereofuscus* BARNES and BENJAMIN, Check list of the diurnal Lepidoptera of Boreal America, p. 21, 1926; reprinted in Bull. Southern California Acad. Sci., vol. 25, pt. 1, p. 21, January-April, 1926 (listed).

*Autochton cellus* ab. *aereofuscus* H. H. SHEPARD, Lepidopterorum Catalogus editus ab Embrik Strand, pars 47, Hesperidae, Subfamilia Pyrginae I, p. 84, Dec. 4, 1931 (listed).

*Diagnosis.*—"Normal specimens of *cellus* and *pseudocellus* are black, or nearly black. The black on this specimen, including the antennae and body parts, is replaced by bronze-brown. The band of gold across the primaries, costal white marks and fringes remain normal. Expanse 46 mm."

*Type locality*.—Baboquivari Mountains, Pima County, Ariz.

*Type*.—A male in the collection of Jean D. Gunder taken on July 15, 1924.

**Var. MEXICANA Draudt**

*Rhabdoides cellus form mexicana* DRAUDT, in Seitz, *Macrolepidoptera of the world*, vol. 5, p. 871, 1922 (diagnosis; Orizaba); pl. 169, row a.

*Autochton cellus var. mexicana* H. H. SHEPARD, *Lepidopterorum Catalogus editus ab Embrik Strand, pars 47, Hesperidae, Subfamilia Pyrginae I*, p. 84, Dec. 4, 1931 (listed).

*Rhabdoides cellus mexicana* HOFFMANN, *Anal. Inst. Biol., Univ. Nac. Mexico*, vol. 3, no. 2, June 1932, p. 139 (Orizaba, Vera Cruz; type collected by Toro II).

*Diagnosis*.—In both sexes with the band across the fore wings almost twice as broad as in the typical form, deep orange yellow, terminating roundedly below, the small apical spots still smaller, reduced to two, the yellow fringes on the hind wings narrower.

*Type locality*.—Orizaba, Vera Cruz, Mexico.

*Type*.—Collected by Cayetano del Toro and sent to Dr. Draudt by Roberto Müller.

**Var. LEILAE A. H. Clark**

Plate 2, figs. 1, 2

*Rhabdoides cellus var. leilae* A. H. CLARK, *Science*, n. s., vol. 80, no. 2068, p. 164, Aug. 17, 1934.

*Diagnosis*.—Very dark, blackish; the usual gold band across the fore wings is replaced by a series of four spots, the first, adjoining the costal border, small, the second, crossing the cell, about half as broad as the usual band in the same place and much lighter in color than the first, the third, very small and bright golden, in the middle of the interspace between veins  $M_2$  and  $M_1$ , and the fourth, nearly as large as the second, in the interspace below near its outer end.

*Type locality*.—Maryland, woods just north of the unpaved portion of the Conduit Road 1.1 miles southeast of Great Falls, or just over one-half mile west of the point where the paved road from Washington turns north up the hill, leaving the conduit.

*Type*.—U.S.N.M. no. 51415; emerged July 20, 1934, from a pupa formed on July 4 and kept under natural conditions. Other specimens emerging later from the same lot were normal.

*Additional specimen*.—W. Herbert Wagner raised a similar individual, but it failed to spread properly and was not preserved.

## KEY TO THE NAMED VARIETIES OF RHABDOIDES CELLUS

- $a^1$ . Band across the fore wings broad and continuous.
- $b^1$ . Ground color black or blackish brown (when fresh).
  - $c^1$ . Band on fore wings normal, golden yellow, pointed below.....*cellus*.
  - $c^2$ . Band on fore wings almost twice as broad as normal, rounded below,  
*mexicana*.
- $b^2$ . Ground color bronze-brown.....*aercofuscus*.
- $a^2$ . Band on fore wings represented by four well-separated spots.....*leilac*.

## VARIATION

This butterfly appears to be unusually uniform in its characters, both locally and throughout its range.

The specimens at hand from Maryland (pl. 2, figs. 3-6), all taken during the past summer, are very dark, blackish, and small. Gunder, speaking presumably of this species as it occurs in Arizona, said that "Normal specimens of *cellus* and *pseudocellus* are black or nearly black." In Maryland a few much lighter badly broken specimens were caught but were not preserved.

The specimens at hand from West Virginia (pl. 1, figs. 7, 8) are as small as those from Maryland, but are lighter in color. They were caught, however, 34 years ago and presumably have faded.

Those from Pennsylvania (pl. 3, figs. 13, 14) are as large as those from Arizona (pl. 3, figs. 11, 12), with which they agree in their ground color as well as in all other details.

At first sight the fringe on the hind wings of the Maryland individuals appears clearer white than it is on the western specimens, but closer examination shows that this is on account of the greater contrast with the darker ground color.

The band on the fore wing varies very little. It is narrowest in two specimens from Kerrville, Tex., but it is almost equally narrow in two from Pennsylvania and in one from Maryland. It is broadest in a specimen from Maryland, though almost equally broad in some from Arizona.

There are no differences that can be detected between specimens from Mexico and others from Arizona. Two from Cuernavaca have the band slightly narrower than the others, and the one from Guatemala (pl. 4, figs. 15, 16) has it slightly broader, though not so uniformly broad as it is in the one from Maryland.

Dr. W. J. Holland said that Mexican specimens are larger and the light band is narrower, and Dr. M. Draudt described a form (*mexicana*) from Orizaba with the band almost twice as broad as usual. It is quite likely that more or fewer of the individuals in certain

localized communities may possess certain minor features by which they may be distinguished; nevertheless, this insect in Mexico as a whole is singularly uniform.

So far as we have been able to determine there are no variations of geographical significance in this butterfly, and the named varieties are therefore to be regarded as individual variants or "aberrations."

#### HISTORY

The first notice of this species was the publication by Dr. Jean Alphonse Boisduval and Maj. John E. Le Conte in 1833 of an excellent colored plate showing the imago, a caterpillar on one of the leaves of a sprig of *Breweria aquatica*, and a pupa. No text was published in connection with the plate, which bore at the bottom the name *Eudamus cellus*.

The plate was a reproduction of a painting by John Abbot, who lived for nearly 20 years—from about 1790 to about 1810—at Jacksonborough, Ga. Jacksonborough no longer exists, but in Abbot's time it was an important town. It was confirmed as the county seat of Scriven (now Screven) County on February 15, 1799, and for more than 40 years the business of the county was mainly transacted there. But in 1847 the public buildings were removed to Sylvania, the present county seat. This robbed Jacksonborough of all importance, and it was soon abandoned.

Jacksonborough was situated on Beaver Dam Creek near its junction with Brier Creek in the north-central part of Screven County, roughly 7 miles north of Sylvania. Presumably Abbot's specimen came from this locality, or its more or less immediate vicinity. The butterfly has not since been reported from Screven County, and until this year the caterpillar that he found has remained the only one known.

In 1837 Carl Geyer published a brief description of this species under the name of *Cecrops festus* (*Papilio gentilis*, *Astycus celebris*), which was illustrated by figures in colors of the upper and under sides.

In the second volume of their "Genera of Diurnal Lepidoptera" published in 1850-1852, Edward Doubleday and John Obadiah Westwood listed this species under the name of *Hesperia cellus*, with the habitat United States.

The Rev. Dr. John Gottlieb Morris, in his "Catalogue of the Described Lepidoptera of North America" prepared for the Smithsonian Institution and published in May 1860, listed *Hesperia cellus*, taking

the name from Doubleday and Hewitson. In his "Synopsis of the described Lepidoptera of North America" published by the Smithsonian Institution in February 1862 Doctor Morris, under *Hesperia cellus*, gave a brief diagnosis of this species, with the habitat United States.

In 1870 Arthur Gardiner Butler proposed the new genus *Spathilepia* in which he included *cellus* as the last of several species listed.

In his "Synonymic Catalogue of Diurnal Lepidoptera" published in 1871 William Forsell Kirby listed both *Spathilepia cellus* and *Thymele festus*.

William Henry Edwards in his "Synopsis of North American Butterflies" published in 1872 included *Spathilepia cellus*, giving as the habitat the Southern States and West Virginia.

One of the unpublished plates of butterflies and moths prepared by Townend Glover shows colored figures of the larva and pupa of this species, and another shows both surfaces of the wings of the imago. They are identified as *Eudamus cellus*, and were copied from the figures of Abbot reproduced by Boisduval and Le Conte.

In the list of the Lepidoptera collected in 1871-1874 in California, Nevada, Utah, Colorado, New Mexico, and Arizona, published by W. H. Edwards in 1875 in the "Report upon Geographical and Geological Surveys West of the One Hundredth Meridian in Charge of First Lieut. George M. Wheeler," *Eudamus cellus* is included, but there is no indication of the locality where it was taken.

In his "Butterflies and Moths of North America" published in 1878 Ferdinand Heinrich Herman Strecker included *Eudamus cellus*, and gave a short synonymy; the range he gave as from Virginia southward to the Gulf of Mexico.

*Eudamus cellus* is included in the "List of North American Macrolepidoptera" prepared by the Publication Committee of the Brooklyn Entomological Society and published by the Society in 1881.

In a revision of the genus *Eudamus* published in 1882 Carl Plötz listed *Eudamus festus*, crediting the species to Hübner instead of to Geyer and placing *E. cellus* as a synonym under it.

Edwards in 1883 recorded *Eudamus cellus* from Arizona, where it had been taken in 1882 by H. K. Morrison either in the vicinity of Fort Grant, Cochise County, or on Graham Mountain.

In his "Revised Catalogue of the Diurnal Lepidoptera of America North of Mexico" published in November 1884 Edwards included *festus* Hübner as a synonym of *Eudamus cellus*, the range of which he gave as West Virginia to the Gulf of Mexico, Texas, and Arizona.



George Hazen French in his "Butterflies of the Eastern United States" published in 1886 gave an excellent description of *Eudamus cellus*, which he said ranges from West Virginia to the Gulf of Mexico, and also occurs in Texas and Arizona.

Regarding the occurrence of this butterfly near Coalburgh, W. Va., W. H. Edwards wrote in 1888:

On one occasion, in June, I visited an unopened coal seam at least a mile from any clearing, and at five hundred feet elevation above the creek, where the coal was exposed to view, owing to its being between two ledges of rock, a little sulphur-tintured water trickled upon the base rock, and here were several [*Debis*] *Portlandia* and that rare butterfly *Eudamus Cellus*, in a cluster, eagerly sucking.

Samuel Hubbard Scudder in 1889 created the new genus *Rhabdoides* for this species and a few others that he did not name. He gave an exhaustive description of the imago but did not figure it. His descriptions of the last stage larva and of the pupa are taken from Abbot's colored figures. He said that it ranges from Georgia to Arizona, and as far north as West Virginia and Kentucky; he also listed a specimen from Tallahassee, Fla., taken by Charles Johnson Maynard on April 17, and another from Putta on the Pacific slope of Mexico about 150 miles from Oaxaca. Scudder said that this species does not seem to be so common as the other larger skippers of the same region and notes that Abbot expressly called it rare. He said that Abbot bred the butterfly on April 25 from a caterpillar that shut itself up in its cocoon 3 weeks previously. He remarked that Abbot said it frequents the sides of swamps, and that in his various manuscripts *Breweria aquatica* is given as the food plant, and upon this it is figured by Boisduval and Le Conte.

Dr. John Bernhard Smith in his "Catalogue of the Insects found in New Jersey" published in the Final Report of the State Geologist of New Jersey in 1890 said that *Eudamus cellus* is taken rarely by the Newark collectors.

*Eudamus cellus* was listed by Dr. Henry Skinner in his "List of the Lepidoptera of Boreal America" published in 1891.

William Beutenmüller in his list of the butterflies of the vicinity of New York published in 1893 gave a brief description of *Eudamus cellus* and figured it; he also gave a description of the caterpillar and of the chrysalis, abridged from Scudder. He said that the food plants are Convolvulaceae and cited Smith's record from Newark, N. J.

Lt. Edward Yerbury Watson listed *Rhabdoides cellus* in his revision of the Hesperiidæ published in 1893.



In their "Biologia Centrali-Americana" published in 1894 Frederick Ducane Godman and Osbert Salvin gave the habitat of *Rhabdoides cellus* as the Southern States, Arizona, and the highlands of Mexico. The Mexican localities given are: Milpas, in Durango (collected by Forrer); Cuernavaca, in June; Xucumanatlan; Omilteme (collected by H. H. Smith); Mexico City (collected by Schumann); Pinal, near Puebla (collected by F. D. Godman); Oaxaca (collected by Fenochio); and Putla (quoting Scudder, who gave it as Putta). They published a figure of the male genitalia.

*Eudamus cellus* was recorded by H. G. White in June 1894 as having been taken in Prospect Park, Brooklyn, N. Y., in 1893, and in November 1895 William Osburn recorded it as rare at Nashville, Tenn., where a single specimen had been taken in August; he said that the food plant is unknown.

Ellison Adger Smyth, Jr., in October 1895 said that *Eudamus cellus* is occasionally taken in the watered ravines in Montgomery County, Va., where the wild catnip covers the ground.

Dr. William Jacob Holland in the "Butterfly Book" published in 1898 gave a brief account of this species under the name of *Achalarus cellus*. He said that what little we know of the early stages is based mainly upon the observations of Abbot, and there is an opportunity here for some young naturalist to render a good service to science by rearing the insect through all stages from the egg. The habits of the larva are not greatly different from those of allied species. He said that *A. cellus* is found in the Virginias and thence southward and westward to Arizona and Mexico, adding that it is common in the Carolinas. He gave an excellent colored figure of the upper surface of a male.

In 1900 Alex. A. Girault wrote that *Achalarus cellus* is abundant in Anne Arundel County, Md.

William Barnes in 1900 said that *Eudamus cellus* is very common in the Huachuca Mountains in Arizona.

Beutenmüller in his account of the butterflies of the vicinity of New York City published in 1902 said that *Eudamus cellus* is exceedingly rare in that region but more common in the Southern States and Mexico.

Harrison Gray Dyar listed *Rhabdoides cellus* in 1902, giving as the habitat the South Atlantic States, Arizona, and Mexico. In a paper published in 1905 he said that it occurs in Arizona.

Speaking of protective coloration of insects in southern Arizona, R. E. Kunze said in 1904 that *Amblyscirtes (Pamphila) bellus* is usually seen feeding on the prominent yellowish cones of *Rudbeckia*

*laciniata*, and is not often observed on any other but this cone-flower. In the Huachuca mountains *Eudamus cellus* is its companion in rifling the yellow flowers of *Rudbeckia*. On these flowers, according to Kunze, *bellus* seems to be less protected than *cellus*.

In their list of the butterflies of North Carolina published in March 1907 Clement Samuel Brimley and Franklin Sherman, Jr., recorded *Eudamus cellus* from Tryon in the extreme southwestern part of the State, where it flies in May, June, and July.

Karl R. Coolidge and Victor L. Clemence wrote in 1911 that in Ramsey Cañon, in the Huachuca Mountains, Cochise County, Ariz., at an altitude of 5,000 to 7,000 feet, *cellus* first appeared about the middle of June but was not plentiful until July. In the same article Dr. J. H. McDunnough said that the collection of Dr. William Barnes contained a specimen of *Achalarus pseudocellus* bearing the label "W. Va." We have examined this specimen and agree with Dr. McDunnough that it is an example of *Rhabdoides pseudocellus*. The label is in the handwriting of W. H. Edwards. Mr. Edwards was not aware that together with *cellus* in Arizona there lives a second smaller species of the same size as *cellus* as it occurs in West Virginia. It is possible that in looking over his collection he saw among the larger Arizona specimens a small individual apparently agreeing with those from West Virginia and, thinking a mistake had been made, changed the label on the latter.

Dr. Henry Skinner in 1911, under *Eudamus (Rhabdoides) cellus*, republished French's description of the imago, and Scudder's descriptions of the last-stage caterpillar and pupa. He gave the range as from West Virginia to the Gulf of Mexico, Texas, Arizona, and Mexico. He repeated the localities given by Scudder, omitting Kentucky, and those given by Godman and Salvin. He added Colima, Mexico, and Nashville, Tenn., August 19 (Osburn). The food plant, he said, is *Breweria aquatica*. He remarked that from the dates of capture it would seem that there are two broods of this species. He quoted Smyth's account of its occurrence in Montgomery County, Va.

In his reprint of Jacob Hübner and Carl Geyer's *Zuträge* published in 1908-1912 Kirby listed *Cecrops festus*, adding the information that the figure represents a female and indicating that the specimen came from Mexico. The distribution of the species is given as North America. Foster H. Benjamin called our attention to the fact that very few of Hübner's species came from Mexico and suggested that the original of *Cecrops festus* was more likely to have come from the eastern United States. We find that Kirby listed only 14 of Hübner's species from Mexico, whereas 117 were listed as from the eastern

United States, 74 of these from Georgia. Though there is no real evidence, we are inclined to believe that the type specimen of *Cecrops festus* came from Georgia and that it was sent to Hübner by John Abbot.

In his list of the Lepidoptera of Florida published in 1917 John A. Grossbeck cited Maynard's record from Tallahassee, originally published by Scudder, and added a new record from Biscayne Bay, where the species had been obtained by Mrs. Annie Trumbull Slosson.

In their "Check List of the Lepidoptera of Boreal America" published in 1917 Drs. William Barnes and James Halliday McDunnough listed this species as *Rhabdoides cellus*.

In 1921 Prof. Arthur Ward Lindsey listed this species as *Cecropterus cellus*, giving a synonymy and saying that it is found in Pennsylvania in July, in Virginia and West Virginia in May and June, and in Texas and Arizona in April and August.

In Dr. Adelbert Seitz' "Macrolepidoptera of the World" Dr. M. Draudt in 1922 gave a short diagnosis and colored figures of *Rhabdoides cellus*, which he said is widely distributed in North and Central America, and described and figured a new variety under the name of *Rhabdoides cellus* form *mexicana*.

In 1925 Jean Daniel Gunder described and figured in colors *Rhabdoides cellus* ab. ♂ *aereofuscus*.

Professor Lindsey in 1925 gave *Eudamus cellus* as the haplotype of the genus *Rhabdoides*.

William Barnes and Foster H. Benjamin in their "Check List of the Diurnal Lepidoptera of Boreal America" published in 1926 included *Cecropterus cellus*, with *festus* Geyer as a synonym and *aereofuscus* Gunder as an aberration.

Dr. William Trowbridge Merrifield Forbes in 1928 listed White's specimen of *Rhabdoides cellus* from Brooklyn, N. Y., saying that it was presumably a stray.

In their revision of the HesperIIDae of North America published in 1931 A. W. Lindsey, Ernest L. Bell, and Roswell Carter Williams, Jr., gave a synonymy of *Cecropterus cellus* and figured the male genitalia. The localities and dates they gave as Pennsylvania, July; Virginia and West Virginia, May to August; Texas and Arizona, April, July-September. They mentioned Gunder's ab. ♂ *aereofuscus*.

In the revised edition of the "Butterfly Book" published in 1931 Holland, under *Rhabdoides cellus*, repeated the information given in the earlier edition, and added that Mexican specimens differ from those from the United States in being larger with the light band narrower.

Lucien Harris, Jr., in 1931 said of *Cecropterus cellus* that this rare butterfly has been taken at Macon, Ga.

In 1932 Carlos C. Hoffmann said that the type specimen of *Rhabdoides cellus mexicana*, described by Draudt in 1922, had been sent the latter by Roberto Müller; it came from Orizaba, Vera Cruz, where it had been collected by Cayetano del Toro.

In his "Butterflies of the District of Columbia and Vicinity" published in 1932 the author recorded *Cecropterus cellus* from the District of Columbia, June 25, 1889 (Ernest Shoemaker); from Difficult Run, Fairfax County, Va., June 23, 1920 (Ernest Shoemaker); and from Collington, Md., July 30, 1930. He said that this species has a wide range throughout the South, but is nowhere very common. It is to be sought for along the sides of streams and in the immediate vicinity of swamps. The species was illustrated by photographs of the upper and under surfaces of a specimen without data.

In August 1934 the author published a brief notice of the discovery of *Rhabdoides cellus* in some numbers in the vicinity of Washington and gave a short account of the eggs and early stages. The eggs and larvae were found in numbers on the hog-peanut (*Falcata pitcheri*). A new form, *Rhabdoides cellus* var. *leilae*, was described. In a note published in October 1934 the locality was given more specifically as near Great Falls, Md.

#### FIELD NOTES

Our observations on this butterfly were made in the woods just north of the unpaved portion of the Conduit Road, 1.1 miles southeast of Great Falls, Md., and slightly more than half a mile west of the point where the paved road leaves the Conduit Road and turns north up the hill. Here a small stream from the woods passes under the conduit. A few hundred feet up this stream north of the conduit there is a cleared spot a hundred feet or so in diameter, along the west side of which, at the base of a steep hillside, the stream broadens into a little marsh perhaps 20 feet across. It was along the edges of this little marsh and in the marsh itself that the great majority of the butterflies were found.

We first met with this butterfly on May 30, when we saw and captured a single individual. On June 3 we caught seven, on June 10 eight, on June 17 ten, and on June 24, when we were accompanied by Dr. George W. Rawson, of Detroit, Mich., we met with no less than twenty. On July 1 we found only four, all of them battered. Two of these were taken home alive, the last dying on July 3.

Previous records for the District of Columbia and its immediate vicinity are: June 23, 1920 (Ernest Shoemaker); June 24, 1925 (F. M. Schott); and June 25, 1889 (E. Shoemaker). These records, combined with our experience, seem to warrant the statement that the maximum abundance is reached about June 24.

We noticed that this skipper is very seldom seen in the morning, appearing only after midday and flying until almost dusk. This habit of appearing in wet hollows near water in the afternoon suggested that the true habitat of the butterfly was somewhere else. Presumably it is active in its home territory during the morning, but in the heat of the afternoon seeks out the wettest places it can find. If it were a swamp or a bog butterfly, as has been supposed, it would certainly be present in wet localities in the morning. All of our swamp and bog butterflies, and all of its relatives in this region, are active in the morning.

Another thing we noticed was that the females soon get the hind wings badly frayed, and old females commonly have the posterior half of the hind wings completely worn away. The prompt fraying of the hind wings of the females appeared to be good evidence that they were engaged in depositing their eggs on some plant, the leaves of which are exceedingly rough on the under side. They were not depositing their eggs on any minutely soft downy plant, such as *Breueria aquatica*, on which the caterpillar was figured by John Abbot, or on any of its local relatives.

In walking through the woods near the marshy expansion of the little stream where we had seen the insect most frequently, we noted a certain spot high up on the hillside where we always saw one or two in passing. Dr. Rawson also found several feeding on *Hydrangea* on the hillside immediately above the stream. Both of these spots are abundantly overgrown with the hog-peanut, *Falcata* (or *Amphicarpa*) *pitcheri*, the leaves of which are extremely rough on the under side, bearing very numerous strong hooked hairs.

On July 1 one of these plants, growing high up on the hillside at the place where in passing we had frequently seen individual examples of the butterfly, was found to be much eaten, and on its larger leaflets we found a score or more of little shelters differing from the shelters described for any of our skippers. In these shelters eight skipper caterpillars were found, in the third, fourth, and fifth stages, differing from any described caterpillars, and we also found the empty shell of an undescribed egg.

On July 4 we collected 167 caterpillars in all stages, 46 empty egg shells, and 6 eggs, all of which hatched a day or two later. Of the



caterpillars brought home, one (collected July 1) pupated on July 4, three on July 8, and two on July 11. We found no butterflies on this date.

On July 15, accompanied by W. Herbert Wagner, we collected 89 caterpillars, all in the fourth or fifth stages, most of them in the latter. As we found a considerable number of large shelters unoccupied, we assume that the usual habit of these caterpillars is when fully grown to leave these shelters and pupate among the dead leaves and rubbish on the ground. We saw no butterflies.

On July 20 a butterfly emerged from the pupa formed on July 4, and on July 25 another emerged from a pupa formed on July 11. The duration of the pupal stage in the summer is therefore 14-16 days.

On August 5, revisiting the locality in company with Dr. and Mrs. William M. Mann and Robert L. Duffus, of New York, we found six butterflies, caterpillars in all stages, and very many abandoned large shelters.

On August 19, in company with Dr. Herbert Friedmann and Hugh Upham Clark, we made a rather intensive search for material, but we found the insect by no means so common as previously. Only 3 butterflies were met with, and we could discover only 39 caterpillars, mostly in the second and third stages with 4 in the first stage and about half a dozen in the fourth; there were no caterpillars in the last stage, but about half a dozen recently abandoned full-sized shelters were found. The numbers of adults and caterpillars of *Epargyreus tityrus* had similarly decreased markedly, and *Achalarus lyciades* was not found in any stage.

On August 26 we were accompanied by Mrs. Frederick V. Coville, Ellsworth P. Killip, and Dr. George S. Myers. We found no butterflies, and only nine caterpillars, two in the first stage, four in the last stage, and three in the fourth stage. About half a dozen recently abandoned full-sized shelters were discovered. A single full grown and very large caterpillar of *Epargyreus tityrus* was found on *Meibomia paniculata*.

On September 1, in company with Dr. and Mrs. William R. Maxon and Miss Alice C. Atwood, we again visited the locality. No butterflies were found, and only 12 caterpillars, 2 in the second stage, 7 in the third stage, and 3 in the fourth stage. A few recently abandoned full-sized shelters were found. It was curious that of the 12 caterpillars found 8 were preparing to molt. One additional caterpillar, in the fifth stage, was discovered with the posterior third of the body blackened by bacterial rot. We had previously found a number of fully grown caterpillars of *Epargyreus tityrus* dead in their shelters

and discolored dark brown, but we had never previously found any evidence that the caterpillars of *Rhabdoides cellus* were attacked by this disease.

In the area in which we found it the butterfly was probably at approximately its maximum abundance, for in midsummer every hog-peanut plant on each of its long trailing shoots harbored at least one group of caterpillars, and usually two or more. On many of the more isolated and peripheral plants and shoots, and on such shoots as climbed high above the general mass, all the leaflets except a few of the largest near the base were entirely destroyed.

On June 1, 1935, W. Herbert Wagner found that the butterflies had reappeared, having survived an unusually severe winter.

The following account of the gold-banded skipper and its early stages is based upon observations on 61 living butterflies, the majority of which were caught, nearly 400 larvae representing all stages collected and brought home, and about 200 eggs and empty egg shells.

#### SEASON

In the vicinity of Washington this butterfly first appears late in May, flies through June, attaining its maximum shortly after the end of the third week, and disappears soon after the first of July. The second brood appears at the end of the third week in July, and the butterfly continues on the wing uninterruptedly, though in constantly diminishing numbers, until about the end of August.

The eggs are deposited over a long period, so that at the time of the disappearance of the first brood unhatched eggs, larvae in all stages, and pupae are to be found.

In July the butterfly is markedly less numerous than in June. Of the six pupae raised in the house three produced butterflies in 14-16 days, and three others remained as pupae until the end of the season. In view of the diminishing numbers of all stages of this butterfly with advancing summer in the field there can be no doubt that in nature, as well as under more or less artificial conditions, a very large percentage of the pupae from caterpillars of the second and succeeding broods last over until the following spring, just as is the case with *Epargyreus tityrus* and *Achalarus lyciades*, and with the local species of *Thorybes* and of *Thanaos* that have a second brood.

The period of emergence of the second brood is very much longer than that of the first brood. But the effect of this on the number of butterflies on the wing at any one time is undoubtedly more than offset by the relatively slight mortality in the younger stages as compared with the heavy mortality among hibernating pupae.



At the end of the season—toward the end of August—most of the very few butterflies still on the wing represent a second brood, while a few represent a third brood.

In Pennsylvania the gold-banded skipper first appears in June, in Maryland and Virginia toward the end of May, in southern West Virginia shortly after the middle of May, and in Georgia, Florida, Texas, and Arizona in April. There are numerous records throughout its range for July, but fewer for August; and only in Texas, Arizona, and southward has it been found in September. Skinner in 1911 noted that from the dates of capture it would appear that there are two broods.

#### HABITS OF THE BUTTERFLY

The gold-banded skipper most frequently is seen in wet grassy areas along the sides of streams or ponds in or near woods. It is seldom to be found in the immediate vicinity of the food plant, though it sometimes feeds on flowers growing near the hog-peanut patches.

Wet open spots in woods seem to form its favorite playgrounds, where the males congregate and engage in combat. This is in interesting contrast to the habit of the males of the local species of the related genus *Thorybes* (*Th. bathyllus*, *Th. pylades*, and *Th. confusus*) which choose as their playgrounds low, bare, and more or less barren hilltops frequently some distance from the nearest food plants, where they are often to be seen playing about in numbers.

We found the gold-banded skipper extremely local. One individual was met with near a temporary pond about 400 yards east of the stream, and another in a marshy spot along another stream about a quarter of a mile west, but these were the only strays we saw.

The flight of this butterfly is low, a foot or so above the ground, or just above the top of the long grass. It is slow and irregular in rounded zigzags with rapid wing beats and occasional short glides (most unusual in a skipper) and is easily followed with the eye, assisted by the bright golden band on the fore wings. Though somewhat jerky, the flight usually lacks the skipping motion characteristic of most skippers; but occasional males when coursing about over the grass tops may exhibit more or less of this. As a rule the flight is short, and the butterfly soon comes to rest, usually on a leaf near the ground or on a level with the grass tops, on a log, or on the ground itself. Rarely it chooses a leaf as much as a yard above the ground. It always rests with the wings fully expanded.

In the woods this butterfly is most inconspicuous, zigzagging about through the undergrowth, always keeping within a foot or so of the ground, occasionally alighting on a fallen dry leaf or on the ground.

It is unsuspicious and not easily frightened. If missed by the net it flies away, but sooner or later returns to the same place, just as the species of *Thorybes* do when on their playgrounds.

It feeds most commonly on the flowers of *Hydrangea arborescens*, which is common on the lower slopes of the hillsides where its food plant grows, but is sometimes seen on the flowers of the button-bush (*Cephalanthus occidentalis*) in bogs near the woods, and on the flowers of the iron weed (*Vernonia glauca*) along woodland paths.

It is the most sluggish, the least suspicious, and the easiest to catch of all our skippers. Even two males engaged in combat seem to take only a half-hearted interest in the proceeding and seldom rise more than a foot or so above the normal flight plane. Their movements as a rule entirely lack the dashing energy of those of the males of other skippers under similar conditions. But on occasion they will develop unsuspected vigor.

In its habits the gold-banded skipper resembles the species of *Thorybes* more closely than it does any other of our larger skippers, but is somewhat less energetic and more retiring, keeping mainly in and near undergrowth. It is at once distinguishable on the wing from *Epargyreus tityrus* and *Achalarus lyciades* by its slower and much less irregular flight, as well as by its habit of keeping always near the ground and dodging through the undergrowth.

But *Achalarus lyciades* is a less energetic flier than *Epargyreus tityrus* and does not fly so high, its flight being intermediate between that of the latter and that of the gold-banded skipper. Indeed, once or twice I have found that what I thought were two belligerent males of *Achalarus lyciades* were in reality males of *Rhabdoides cellus*.

#### EGGS

Plate 4, fig. 17; plate 6, figs. 28, 29; text figs. A-D, p. 26

The eggs are fastened on the under side of the leaflet in its outer half. They are usually nearer the midrib than the edge, and are always placed in the intervals between the veins, where they are pressed down upon and glued firmly to the short hooked bristles. Although most of the eggs are found in the middle third of the leaflet, longitudinally, a few are nearer the edge. But they are always in the outer half of the leaflet, and between the veins.

The eggs are laid almost invariably on the large leaflets toward the base of the plant and are only exceptionally found on the small leaflets near the summit. More or less isolated plants, and especially those growing along paths or open spots, are preferred to those growing in

dense masses, and on these the earliest caterpillars of the season are to be found. As the season progresses and the caterpillars become more numerous, the butterflies work inward from the periphery toward the center of the masses of hog-peanut until every plant bears its quota of caterpillars.

Though single eggs are commonly found, most of the eggs are deposited in groups of two or three. Strings of four are frequent and strings of five (pl. 4, fig. 17) occasional. One string of six was found. Sometimes two eggs are found side by side and unattached, presumably laid by different females. One leaflet was discovered which bore seven eggs in one group of three and two groups of two each.



Eggs of *Rhabdoides cellus*.

FIGS. A-D.—A, egg with 17 ribs, lateral view. B, egg with 17 ribs, apical view. C, egg with 18 ribs. D, egg with 19 ribs. All the eggs have the micropylar portion chipped away. See also plate 3, fig. 17, and plate 5, figs. 28, 29.

When the eggs are deposited in strings, the second egg is placed between the equator and the pole of the first so that the vertical axes of the two eggs make an angle of roughly  $120^\circ$  with each other, and the third is placed on the second in the same way. The little egg strings are thus very irregular, but only the first egg is fastened to, or touches, the leaf.

The eggs (pl. 4, fig. 17; pl. 6, figs. 28, 29; text fig. A, p. 26) are subglobular, 1 mm in diameter, very nearly as high as broad, broadest shortly above the base, with the upper portion very regularly and broadly rounded and the broad flattened base slightly concave in the center and rounded at the borders.

The sides are marked with prominent vertical ribs (figs. A-D, p. 26) that vary from 15 to 21, but are usually 17 and commonly 18, in number. In 152 eggs the number of ribs was as follows: 15 (4); 16 (33); 17 (56); 18 (45); 19 (12); 20 (1); 21 (1). Expressed in percentages the figures are approximately as follows: 15 (2.6 percent); 16 (22 percent); 17 (37 percent); 18 (29 percent); 19 (7.8 percent); 20 (0.6 percent); 21 (0.6 percent).

Irregularities in the ribs are infrequent, only three cases having been found. One egg with 19 ribs has an additional incomplete rib extending from the apex to a short distance beneath the shoulder. Another egg with 19 ribs has an incomplete rib that extends upward from the base to a short distance beneath the shoulder. A third egg with 16 ribs has an incomplete rib that extends from the base half way up to the shoulder. The ribs on either side of this incomplete rib bend toward each other beyond it so that at the shoulder they are the same distance apart as any two of the other ribs. The second rib to the left of the incomplete rib forks just beneath the shoulder, the right branch joining the rib to the right at the shoulder.

The ribs run from the upper portion of the curved border of the flattened base upward to the summit. In the lower half of the egg they are low, narrow, and inconspicuous, but they increase in height, width, and prominence above the equator. In fresh eggs the ribs above the equator may bear long irregular glassy hairs that soon wear off.

The ribs are connected by very fine transverse lines placed very close together, the oblong interstices between them over most of the surface being roughly 8 to 10 times as long (transversely) as broad, but becoming shorter toward the summit. In the lower half of the egg these transverse lines are so faint as to be obsolescent; in the upper half they become more definite, higher, and somewhat more widely spaced. Above the equator where the transverse lines join the vertical ribs they become suddenly and greatly expanded so that the ribs appear to be prominently and evenly beaded.

The apical portion of the egg for an area about 0.5 mm in diameter, or about half the diameter of the egg itself, is occupied by a conspicuous irregular reticulation. Alternate ribs are continued to the micropylar basin at the summit of the egg. Between these are usually three stout and widely spaced transverse bars as high and conspicuous as the ribs themselves. Some of the ribs here commonly fork, so that the reticulation is composed of quadrate, triangular, rhombic, and five-sided figures usually of more or less equal area. The ridges of this reticulation, including the continuation of the ribs within this area, are narrower and lower than the ribs beyond, smooth, high, abruptly differentiated from the smooth surface of the egg, and very conspicuous. The apex of the egg is occupied by a small flat circular micropylar basin.

The eggs are yellow, becoming brownish yellow before hatching. They are translucent, so that the head of the caterpillar is easily seen through the thin shell. The empty egg shells are translucent white with more or less of a pearly luster.

## FIRST-STAGE CATERPILLAR

Plate 6, fig. 30; plate 8, figs. 43, 49, 50

On issuing from the egg the caterpillar of *Rhabdoides cellus* is 2 mm long and has a disproportionately large head 0.7 mm in width.

The head is finely and evenly rugose and bears a few widely scattered long bristles. The ocelli are six in number, four of them equally spaced in a curved line, one directly back of this line on the same level as the space between the second and third in the line counting from the top and distant from the line about half its length, and the sixth behind and below the others, "southwest" of the lower end of the line on the right side and "southeast" on the left, and distant about the length of the line from the its lower end.

The dorsal shield on the first thoracic segment is large and conspicuous with broadly rounded ends that reach about half way down the side of the segment. Its longitudinal length in the middorsal line is equal to about half the length of the head at the same level. It bears a bristle near the anterior edge half way between the middorsal line and the end, and another half way between this and the end near the posterior edge.

The first thoracic segment bears on either side a single very long hair curving anteriorly.

The legs of the first thoracic segment are darker and more corneous than the others.

Each segment behind the first thoracic bears two long hairs near the ventrolateral margin and one above the spiracle, or, if a spiracle is not present, in the corresponding position.

Dorsally each segment bears four well-separated minute papillae each supporting a short, straight, blackish, apically enlarged bristle, there being four rows of these down the back, the two inner rows very regular, the two outer more or less irregular.

The terminal segment bears on each side of the median line two long hairs near the distal border of the dorsal surface, and two below.

The prolegs have two long hairs on the outer side.

The spiracle of the eighth abdominal segment is very much larger than the minute spiracles on the other abdominal segments, and is situated about twice as far above the ventrolateral border.

The anal aperture has below it a conspicuous long wedge-shaped fan terminating in a comb of long, dark, tapering, stiff bristles.

The head is light yellow brown, the mouth parts margined with narrow lines of darker, and the bases of the ocelli darker. The dorsal shield is deep maroon, the rest of the first thoracic segment pink. The body is chrome yellow.



## SECOND-STAGE CATERPILLAR

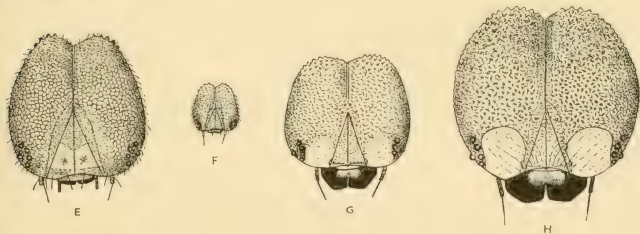
Plate 6, figs. 31, 32; text fig. E, p. 29

The head capsule is 1.1 mm wide at the widest part.

The head is more coarsely rugose than in the first stage. On the summit of the lobes are several well-separated, scalelike, more or less thin, sharply pointed triangular processes standing directly upward or leaning slightly forward. The hairs are much more numerous than in the stage preceding, but shorter. They are longest about the mouth parts.

The short, blackish, apically enlarged bristles with flaring ends standing on conical papillae are much more numerous on the dorsal surface than in the first stage, and more irregularly scattered.

The lower portions of the sides of the segments below the stigmata bear numerous short hairs.



Heads of second- to fifth-stage caterpillars of *Rhabdoides cellus*.

FIGS. E-H.—E, second stage. F, third stage. G, fourth stage. H, fifth stage. Figs. F-H are all on the same scale, much less magnified than fig. E. The head of the first stage is shown on plate 7, figs. 49, 50.

The sides of the prolegs bear numerous short hairs.

The end of the body bears numerous hairs of various lengths, though none of them are very long.

The head is deep maroon, almost black, without markings. The first pair of thoracic legs is dark, almost as dark as the head, but the others are of the same color as the body.

The maximum size for this stage is 8 mm in length.

## THIRD-STAGE CATERPILLAR

Plate 6, fig. 33; text fig. F, p. 29

The head capsule is 2 mm wide at its widest part.

The scalelike prominences on the summit of the head lobes are more numerous than in the preceding stage, and the hairs are also more numerous.



On the dorsal surface the short bristles with enlarged ends are more numerous, and lighter in color. These also extend down the sides to below the spiracles. Below these along the inferolateral border of the segments are numerous hairs of moderate length.

The prolegs bear numerous hairs of moderate length.

The head is almost black, and is unmarked. The first pair of true legs is darker than the others.

The maximum size for this stage is 12 to 13 mm in length by 2.7 mm in width.

#### FOURTH-STAGE CATERPILLAR

Plate 6, fig. 34; text fig. G, p. 29

The head capsule is 3 mm wide at its widest part.

The total length of freshly molted caterpillars just entering this stage is 12 to 13 mm.

The head is as in the stage preceding, but more densely hairy, the hairs curving downward and being longest in the vicinity of the mouth parts.

The thoracic shield bears numerous scattered hairs.

Beyond the abruptly truncated end of the thoracic shield, extending downward to in front of the upper portion of the large oval spiracle, is a triangular plate, more or less definite, with the downward pointing apex very broadly rounded, representing the detached end of the shield, from which it is separated by a rather broad channel.

The dorsal surface is thickly beset with short, fine hairs, more or less of the ordinary form, which become longer and finer along the lower lateral margins of the segments, and longer and stouter at the end of the body.

The prolegs bear numerous fine hairs which become thickly crowded and curved downward toward the foot.

All of the circular indurated spots described for the last (fifth) stage are present.

The color is as in the following stage, except that the head is somewhat darker and the large spots, now appearing for the first time, are vague and ill-defined and shade imperceptibly into the surrounding color.

When the first thoracic segment is swollen preparatory to molting, a broad, elongated deep chrome spot appears extending backward and diagonally outward from under the necklike posterior extension of the head capsule on either side at the dorsolateral margin.

The maximum size of this stage is about 22 mm long by 4.5 mm wide.

## FIFTH-STAGE CATERPILLAR

Plate 6, figs. 35, 36; plate 8, figs. 44-48, 51, 52; text fig. H, p. 29

The head capsule is from 4.3 to 4.8 mm wide at the widest part, slightly below the middle, and 4.8 mm high from the tip of the mandible to the summit of the lobe on the same side.

The total length of freshly molted caterpillars just entering this stage is about 23 mm. They will pupate when 24 to 25 mm long and 5 mm broad. Fully fed caterpillars are 32 to 35 mm long and unusually slender for caterpillars of this group, being only 5 to 6 mm broad. The largest one found was, when resting, 30 mm long and 6.7 mm broad.

The head at the summit of the lobes is minutely roughened with fine, more or less irregular vermiculations. Among these are numerous well-separated, abruptly elevated mesa-like elevations with the flattish top sloping upward and forward, or on the upper part of the front of the head outward and downward. From the edge of the top of these mesa-like elevations 6 to 8 or more fine but prominent ridges run downward and, turning outward, join the general fine vermiculation of the surface. These abrupt elevations, finally becoming irregular rugose tubercles, run down the sides of the head to the mouth parts. The front of the head below the upper portions of the lobes is closely vermiculated with very fine ridges which at first are here and there gathered into knots, but lower down become evenly disposed over a minutely rugose surface. Above the large yellow spots in the vicinity of the frontal triangle and also over the spots themselves the ridges become parallel and well spaced and run downward and inward toward the frontal triangle, making with it an angle of about 60°. Just above the apex of the frontal triangle and on each side of the median groove there is an irregular shield-shaped area with a small circular elevation in the center. There are two more similar circular elevations lower down, one on either side of the frontal triangle. On the frontal triangle there is a fine but prominent median ridge which in its upper quarter is somewhat sinuous with side branches running off from it, but in its lower three-quarters is straight and regular with a broad bare space on either side. Two or three of the lines over the yellow spot run into the frontal triangle, here bending downward and running parallel with the median carination to the lower edge. The head is thickly beset with slender hairs curving downward. These become erect on the frontal triangle, and over the yellow spots project downward and inward toward the mouth parts. The ocelli are arranged in a curved line of four along the outer concave edge of the yellow spot, with a fifth opposite the middle of the row forming with the first and third

in the curved row, counting from either end, approximately an equilateral triangle.

The shield on the first thoracic segment bears numerous short hairs. The detached ends of the thoracic shield are enclosed with the rest of the shield in a thick pad of skin and are not readily identifiable.

Above the anterior to the large prothoracic spiracle, in the center of the detached end of the thoracic shield, is a small, smooth, circular indurated spot surrounded by a circle of well-spaced hairs which are distant from it somewhat more than its own diameter. This spot is directly "northeast" of the spiracle on the right side, and "northwest" on the left. It is distant from the spiracle nearly the longer (vertical) diameter of the latter and lies in a vertical plane about its shorter diameter in advance of it.

There is another similar but less conspicuous spot below this, directly in front of the middle of the spiracle.

Directly beneath this, near the ventrolateral border of the segment and over the base of the first pair of thoracic legs, are two similar but larger spots with a diameter nearly twice as great. These are distant from the spiracle nearly twice its greater diameter and are about half their own diameter apart. One of them is higher than, and in advance of, the other.

Below and anterior to the first abdominal spiracle—"southeast" on the right side and "southwest" on the left—and distant from it about its shorter diameter is a similar spot of the same size as the two last mentioned. On the segments following, this spot is considerably lower, being distant from the spiracle about twice its longer diameter, the distance slowly increasing as the spiracles gradually decrease in size posteriorly. On the eighth abdominal segment the spot is directly beneath the enlarged spiracle, which is situated at a higher level than the spiracles preceding, and is distant from it nearly twice its longer diameter.

In the middle of the outer side of the large middle segment of each of the prolegs is a similar, but smaller, spot, that on the terminal prolegs being larger than the others.

On the ventral surface there are two similar spots on each of the two first abdominal segments situated one on either side on a line between the middle of the bases of the last thoracic legs and the first prolegs, and there are two similarly situated on the segment between those bearing the fourth pair and the terminal prolegs. There are also two on the dorsal side of the last segment.

The body is clothed with very numerous but well-spaced short, fine, pointed hairs, among which are numerous much longer, scattered,

slender, and pointed transparent hairs that become somewhat more numerous on the lower lateral borders of the segments, and much more numerous and darker on the dorsal surface of the last segment. The prolegs bear numerous down-curved hairs about the foot, and many on the basal portion.

The ventral surface has rather numerous scattered hairs.

The anal fan (pl. 8, fig. 52) is long wedge-shaped, ventrally gently convex, with 18 long, tapering, blunt teeth about the rounded distal edge. From the base of each of these teeth a rounded ridge runs to the narrow base.

The head in this stage resembles very closely the head of *Epargyreus tityrus*, differing chiefly in its smaller size, in the longer and more numerous hairs with which it is clothed, in its darker color, and in its yellow instead of orange spots.

The head is claret brown with a large deep chrome spot between the frontal triangle and the ocelli on either side. The border of the chrome-yellow spot adjoining the ocelli is gently concave, following the curved line along which the ocelli are placed, the inner border is evenly rounded, and the upper and lower borders are flattened. The mandibles and antennae are shining black.

The first thoracic segment bears a smooth clay-colored dorsal shield narrowly bordered in the middle third of the anterior margin with olive buff. A fine line of olive buff runs across it in the middorsal line of the caterpillar. A narrow groove near the posterior margin of the shield running not quite to the ends on either side is darker in color than the rest of the shield. The remainder of the first thoracic segment is bright rose red, or rose red below and straw yellow above, the two colors being divided by a line running from the lower portion of the sides of the neck just behind the head backward and upward to a point on the second thoracic segment at the level of the end of the thoracic shield.

The dorsal portion of the body is apple green with numerous evenly distributed small sulphur-yellow dots which are darkest in the anterior third, gradually becoming paler posteriorly.

The dorsal surface is delimited by a conspicuous broad lateral line of clear sulphur yellow. In the middle of the body this line is somewhat wider than the height of the deep chrome spots on the head, but it tapers to less than half this width at either end. The line is in reality interrupted, being composed on each segment of an irregularly bounded, but more or less squarish, mark followed by a broad vertical dash of the same height or slightly higher, which in turn is followed by three narrower vertical lines of the same length or slightly longer.

The sides of the body below the sulphur-yellow lateral line are apple green, somewhat lighter than the dorsal surface except in an indefinite band just below the lateral line and of about the same width. They bear numerous evenly distributed small sulphur-yellow dots.

The under surface, including the prolegs, is apple green, but paler, clearer, and more translucent than the upper surface, and without any yellow dots. The posterior end of the body and a narrow and ill-defined line just above the prolegs are pale, like the under side.

The thoracic legs, which at this stage are all alike, are straw yellow, becoming faintly brownish at the tip.

#### DURATION OF THE EARLY STAGES

We regret that it was not possible to determine the length of time spent by the larvae in each stage or the length of time spent in the egg, but the food plant is not one that lends itself to transplantation to or cultivation in a city house or garden.

The elapsed time between the appearance of the first brood (May 30, or perhaps a few days earlier) and the first appearance of the second brood (July 20) is 50 days, or slightly over 7 weeks. Two weeks are spent in the pupa, so that the period from the laying of the eggs to the formation of the pupa is 5 weeks, or a few days more.

#### MOLTING

The molting from the fourth to the last stage may be described as follows. Caterpillars preparing to molt are easily distinguishable by their swollen first thoracic segment. This becomes more and more distended until the skin tears apart just back of the thoracic shield. The lobes of the new head emerge from the rapidly widening slit, and in a few minutes the old head capsule with the thoracic shield attached drops off.

The new head is at first very pale dull greenish yellow against which the large chrome yellow spots, much darker, stand out prominently. The head very soon begins to darken, and within two hours has become a rather deep reddish flesh color.

After a resting period of considerable duration the caterpillar crawls out of the old skin, which is left extended at full length on the floor of the shelter.

The other molts do not seem to differ from this, except that in the molt from the first to the second stage the head capsule breaks away from the skin of the body along its posterior border, leaving the thoracic shield attached to the body skin.



An interesting feature of the molts is the striking uniformity in the sizes at which the various molts take place in different caterpillars. Fifty or more molting caterpillars were measured, and the difference between any two at the same stage was found to be negligible.

#### HABITS OF THE CATERPILLAR

The caterpillars of this species, like the adults, are more sluggish than the corresponding stage of *Epargyreus tityrus* or of *Achalarus lyciades*. If caterpillars of these three species are placed together, those of the last two will be the first to escape. They are also much less excitable, and although they will sometimes on being disturbed spit out a copious green liquid, or turn suddenly and attempt to bite, such actions are very exceptional. Indeed, the placidity of these caterpillars stands in strong contrast to the irritability of the caterpillars of *Epargyreus tityrus*.

The caterpillars remain concealed within their shelters during the day, those in the first three stages clinging to the roof with their head in the apex, those in the last two stages resting on the floor. In the first two stages, especially in the first, they are more or less restless, sometimes wandering about within their shelters and occasionally protruding the head from under its edge for a second or so, but the larger caterpillars remain quite inert.

At or just before dusk the caterpillars begin to leave their shelters to feed. Those in the first two stages may be seen crossing to the opposite side of the leaflet, and those in the third stage traveling to another leaflet. The caterpillars in the last two stages appear to be more cautious and to commence feeding later, as none of them were seen in the field outside their shelters. In the house, however, they fed voraciously after dark, consuming wilted and even dry leaves if no fresh leaves were available.

The caterpillars will live together in harmony under the most crowded and adverse conditions, displaying no tendency toward cannibalism.

#### SHELTERS

Plate 7, figs. 37-42

On escaping from the egg, the caterpillar eats away the central portion to within a short distance of the profile of the egg as seen from above. It then protrudes its head, directly upward, for a distance of about 0.5 mm and remains in this position for a few hours without moving. Then somewhat suddenly it crawls from the egg, travels to the edge of the leaf, and begins to construct its first shelter.



The shelters made by the young caterpillars (pl. 7, figs. 41, 42) are very characteristic. In the leaflet a cut is made running diagonally in from the edge, the inner end of the cut being nearer the base of the leaflet than the outer. Then nearer the base of the leaf a second cut is made, much shorter than the first, running inward at right angles to the edge of the leaflet to a point near the inner end of the first cut. The wedge-shaped flap thus formed is then turned inward over the upper surface of the leaflet (see pl. 7, fig. 40). The caterpillar now draws the two ends of the short edge of the flap toward each other and fastens the free angle to the surface of the leaflet near the inner end of the cut so that this border, originally the shorter edge of the flap, forms a high narrow arch. Beginning at the top of the arch the caterpillar fastens the sides of the highly arched opening tightly together, working downward as far as possible toward the bottom, but always leaving a low-triangular opening at the bottom (pl. 7, fig. 39). The acute angle formed by the edge of the leaflet and the longer cut is now fastened down to the surface of the leaflet as far away as possible from the edge of the leaflet, so that the edge of the longer cut and that edge of the flap that was originally the edge of the leaflet lie close down upon the upper surface of the leaflet. The only portions of the flap that are fastened to the surface of the leaflet are the angles between the original outer edge of the leaflet and the two cuts.

The result of this operation is a shelter that in shape resembles a limpet with the apex of its shell near one end, or a broad cone cut very diagonally. The apex of this structure was originally the middle of the shorter cut in the leaflet, now folded together.

The apex or peak of the shelter is secured by a broad and very dense mass of silk, and a very dense band closes the opening in front. At each end of the line forming the hinge where the bending of the flap over the upper surface of the leaf takes place there is a large amount of silk in a dense band forming a sort of bracket that holds the flap in the proper position over the upper surface of the leaflet. These two brackets are commonly connected by a close network of silk running from one to the other—that is, along the line of folding. A broad and rather dense network of silk is run down the middle of the roof of the shelter to furnish a footing for the caterpillar when resting during the day. The whole floor of the shelter is covered with a fairly close network, the caterpillar working inward from the edges, where the silk is laid down most thickly. This last network has the effect of making the floor of the shelter concave, thus giving more room within it.

The entire roof of the shelter is sometimes lined with silk, but in this case the band down the middle is always much more dense than the rest.

To recapitulate, the densest bands of silk are spun (1) in the peak of the shelter, (2) down the anterior part of the shelter, and (3) at the ends of the line of folding. All these bands are so strong that if the shelter is pulled apart the leaflet will tear around their ends. They are responsible for the form and for the security of the shelter. They are so very much stronger than the few threads used to fasten the angles of the flap down upon the surface of the leaflet that when these are cut after the abandonment of the shelter, the latter retains its form and is quite indistinguishable, unless touched, from an inhabited shelter. The broad network down the middle of the top of the shelter is considerably more dense than the relatively open, though complete, network that covers the floor of the shelter and makes it concave; this last is more dense peripherally than in the central portion.

The caterpillar enters and leaves the shelter under the inner edge—that is, the edge toward the middle of the leaflet. Within the shelter it always rests on the under side of the roof extended at full length with its head in the apex of the cone.

The path of the caterpillar from the shelter to the feeding area on the opposite border of the leaflet or in the later stages on another leaflet is marked by a runway of irregularly zigzag silk threads.

The original shelter is occupied for only a short time. It is then abandoned, first being rendered useless by the cutting of the threads that hold the flap down upon the upper surface of the leaflet. A second shelter is made which is abandoned and rendered useless in the same way, and others follow suit.

The first two shelters are usually made on the same side of the same leaflet, the second nearer the base than the first. The third is either on the other side of the same leaflet, or upon an adjoining leaflet. The large shelters of the third-stage caterpillars are always solitary, each on a leaflet by itself.

A single leaflet will commonly have three or four shelters along the margin of its outer half, but sometimes more are found, and on one leaflet we found no less than eight.

As the eggs are deposited usually two or three to a leaflet, the shelters nearest the base of the leaflet on each side are commonly occupied, the others empty. Sometimes three caterpillars are found on a single leaflet, though this is unusual. As a rule only two caterpillars will be found on a single leaflet, the others, if there are more than two eggs in the string, going to the adjacent leaflets.

The small caterpillars build their shelters progressively basalward from the apex of the leaflet, though never in its basal half. As they become larger they descend to the larger leaflets lower down.

As a result of the habit of the caterpillars of partially destroying abandoned shelters, occupied shelters are easily distinguished from unoccupied ones, a slight touch sufficing to raise the latter from the surface of the leaflet.

On a single occasion we found a second-stage caterpillar in a shelter made by fastening together two small overlapping leaflets after the fashion of the caterpillars in the last stage.

After entering the fourth stage the caterpillar constructs a shelter of a different type. Sometimes two long cuts are made running directly inward from the edge of the leaflet about an inch apart, and the outer edge of the flap so formed is simply folded inward over the upper surface of the leaflet and fastened down along the inner edge forming a cylindrical shelter more or less broadened in the middle. More commonly, perhaps, the margin of the leaflet is simply folded inward without any cuts being made. Whereas the shelters described previously are always in the outer half of the leaflet, these shelters are always in the broadest portion.

This type of shelter is soon abandoned, and the now large caterpillar binds two superposed leaflets together by a series of stout silk bands having the form of an elongate oval from 1 to 2 inches in its longer diameter. Within this oval both leaflets are lined with a sparse silk network, most dense about the periphery, that pulls their surfaces into a rather strongly concave form resulting in a well-concealed and commodious home.

Occasionally any convenient leaf may be fastened to the upper surface of a hog-peanut leaflet, or the shelter may be made of the leaves of the plant about which the hog-peanut is twining. Thus we have twice found large caterpillars in a shelter made by fastening a golden-rod (*Solidago*) leaf securely down upon a hog-peanut leaflet, and we have found others in shelters made of a hog-peanut leaflet and an oak leaf, two hickory leaflets, two sassafras leaves, and two grape leaves.

#### SHELTERS MADE BY RELATED SPECIES

On July 4 we found, together with the caterpillars of this species, a number of the caterpillars of *Epargyreus tityrus* on the larger leaflets of *Meibomia* (or *Desmodium*) *paniculata*, and on the leaflets of *M. dillenii* and the much less common *M. michauxii*. They were especially common on the first named. They were also abundant on the

leaflets of *Robinia pseudacacia*. With these on *Meibomia paniculata* and on *M. dillenii* we also found, in much smaller numbers, the caterpillars of *Achalarus lyciades*.

The caterpillars of both these species were in all stages, from those just hatched to the fully grown. The caterpillar of *Rhabdoides cellus* is easily distinguished from that of the other two species by its apple-green color and especially by the broad bright yellow lateral line.

The shelters made by the small caterpillars of *Epargyreus tityrus* and of *Achalarus lyciades* are alike, but they differ from the shelters made by the small caterpillars of *Rhabdoides cellus*. A long slit is made in a leaflet running inward at an angle more or less approximating  $45^\circ$  with the edge for a distance of about 6 mm. Then about 8 mm nearer the base of the leaflet another cut is made more or less at right angles to the edge of the leaflet to a depth of about 5 mm. The inner ends of these two cuts are 2 or 3 mm apart. The flap formed by these cuts is now bent inward over the upper surface of the leaflet and fastened down at the angles formed by the cuts and the outer margin of the leaflet. The two cut edges are left unfastened. The caterpillars of *Epargyreus tityrus* and of *Achalarus lyciades* enter and leave the shelters through the lenticular openings at the ends, whereas those of *Rhabdoides cellus* enter and leave the shelters under the long inner edge.

The shelters of the small caterpillars of *Rhabdoides cellus*, looking like little green limpets along the edge of the hog-peanut leaflet on the upper side, are at once distinguishable from the slightly and evenly convex shelters of the similarly small caterpillars of *Epargyreus tityrus* and *Achalarus lyciades*.

In the last stage the caterpillars of both *Epargyreus tityrus* and *Achalarus lyciades* make their shelters quite after the fashion of those of *Rhabdoides cellus*, at first folding inward a portion of the leaflet between two well-spaced cuts and fastening it down, and later, when they have become large and heavy, fastening two leaflets together. On *Robinia pseudacacia* the larger caterpillars of *Epargyreus tityrus* fasten together from two to eight, usually four or six, of the small leaflets.

We have never found the caterpillars of *Rhabdoides cellus* on any plant other than the hog-peanut. Though we have found hundreds of the caterpillars of *Epargyreus tityrus*, we have never found but one on the hog-peanut in this region. This was a fully grown one in a shelter formed of two leaflets, and it may possibly have strayed to the hog-peanut from some other plant.

However, on Apple Orchard Mountain in Bedford County, Va., we have found the caterpillars of *Epargyreus tityrus* frequently on the small-leaved hog-peanut (*Falcata comosa*), and they have been reported by others as found on the same plant.

#### POSSIBLE CORRELATION BETWEEN THE TYPE OF SHELTER AND THE TEXTURE OF THE LEAVES

It is possible that the very delicate texture of the hog-peanut leaflets, rather than any inherent peculiarity of the young caterpillars of the gold-banded skipper, is responsible for the construction of the peaked shelters. Some insect larvae show great ingenuity in adapting themselves to changed conditions.

The leaflets of the hog-peanut are less firm than are those of the species of *Mcibomia*, *Robinia*, etc., upon which the caterpillars of *Epargyreus tityrus* and of *Achalarus lyciades* usually are found. Indeed, they are so delicate that unless the little shelters were braced in some way they would scarcely support the weight of a caterpillar clinging to the roof.

If the peaked shelters are simply due to the delicate texture of the hog-peanut leaflets, then the caterpillars of *Rhabdoides cellus* when on plants with firmer leaves would construct shelters of the same type as those of *Epargyreus tityrus* and of *Achalarus lyciades*, and these species on the hog-peanut would make their shelters after the fashion of those of *Rhabdoides cellus*.

On examining our series of second stage caterpillars after preservation in alcohol, two or three caterpillars of *Epargyreus tityrus* were found among them. Now if these had been in the type of shelter usually made by this species this would certainly have been noticed in the field. But they were not recognized until after preservation. The inference is that they were found on the hog-peanut living in peaked shelters of the type formed by the caterpillars of *Rhabdoides cellus*. But actual proof is lacking.

Elsewhere we have found the young caterpillars of *Epargyreus tityrus* on the small-leaved hog-peanut, always in its usual type of shelter. The leaflets of this plant, however, are of a firmer texture than the large leaflets of *F. pitcheri*.

#### COCOON

The fact that we have found a large number of abandoned shelters made by fully grown caterpillars, but have never found a pupa in a shelter, leads us to believe that the caterpillars leave the shelters and pupate among the dead leaves on the ground.



We have found the pupae of *Epargyreus tityrus* in the last stage shelter, but never the pupae of this species.

In forming their shelters the largest caterpillars fasten one leaflet down upon the upper surface of another in such a way as to leave an oval cavity about an inch long and of considerable depth between them. The leaflets are fastened together by strong bands of silk 2 to 6, usually 3 or 4, mm apart. These shelters are not destroyed when they are abandoned, and therefore are frequently appropriated by spiders or serve as more or less temporary abiding places for various types of insects.

In captivity the cocoon is formed after the fashion of the shelter of the fully grown caterpillar but is much more elaborate. Two suitable dry leaves are fastened together in such a way as to leave between them an oval cavity nearly or quite an inch long and of considerable depth. The stout bands of silk by which the leaves are fastened together are usually 3 or 4 mm apart, though sometimes closer together and sometimes more distant. They are stouter than the bands used in fastening the leaves together for the last shelter.

If the leaves are broken so that an aperture of appreciable size is left this aperture is closed by long bands of silk (pl. 4, fig. 18) usually 3 to 4 mm apart, though sometimes closer and sometimes distant as much as 6 mm, between which are run more or less regular cross bands approximately the same distance apart, forming an irregular network. The caterpillar then broadens the bands and cross bands until some of the interstices are wholly closed and most of them are reduced to a rough circle of varying dimensions.

This broadening of the bands and cross bands is simply a part of the process of lining the whole interior of the cocoon with a fairly uniform irregularly crisscross loose web of silk that scarcely conceals the underlying leaf and becomes dense only about the spot where, when it finally comes to rest, the caterpillar attaches the terminal pair of prolegs.

If the caterpillars are too crowded one may drive out another from a partially completed cocoon and appropriate it for itself, or part of a cocoon may be eaten away by caterpillars not yet fully fed. But these caterpillars are never cannibalistic.

#### PUPATION

Just before pupation the largest larvae shorten to a length of about 24 mm. The body becomes swollen to a maximum width of about 7 mm, the skin becoming very taut so that the plications on the



segments disappear. The second thoracic segment, which ordinarily is of about the same size as the third, becomes enormously swollen so that it is larger, though not broader, than the last thoracic and first abdominal segments together, and the skin covering it becomes exceedingly taut.

The color changes to a fairly uniform apple green, somewhat deeper green on the second thoracic and last three abdominal segments and slightly more yellowish elsewhere. The conspicuous yellow lateral stripe and the yellow spots completely disappear. The bright pink of the first thoracic segment fades to a light putty color with scarcely a trace of pink, and the brilliant chrome spots on the head fade to a dull deep putty color and become inconspicuous.

After a quiescent period of about 2 days the head splits along the median groove between the epicrania and down the suture between one of the epicrania and the adjoining adfrontal. The dorsal thoracic shield splits across in the middorsal line, and the skin of the dorsal surface splits down the median line as far as the fourth abdominal segment, or just above the second pair of prolegs. By intermittent wriggling the larval skin is shoved backward and compressed into a small bundle at the end of the body, drying out with extraordinary rapidity during this process. By further wriggling the cremaster is freed from the larval skin and entangled in the button of silk on which the posterior prolegs of the caterpillar previously rested.

#### PUPA

Plate 5, figs. 19-25

Immediately after its formation the pupa is a brilliant transparent green on the wing covers and thorax, with the abdomen a very light yellow clay color, almost straw yellow, becoming greenish at the tip. The eye is bordered posteriorly with a curved row of small bright red spots. Between the prothoracic spiracles are two fine transverse lines of bright red, one on either side of the median line. The anterior border of the thorax is pinkish. The prothoracic spiracles and the cremaster are dark brown, the former soon becoming blackish.

Within an hour the pupa begins to darken, the abdomen and head becoming gradually yellow brown and the wing covers and thorax olive green, darkest on the dorsal portion of the thorax and the anterior half of the wing covers below. In about 4 hours the abdomen has become orange brown, darkest posteriorly, the head orange brown with a tinge of olive green, and the thorax and wing covers bright olive green, lightest on the posterior half of the wing covers ventrally.

Continuing to darken, the head, thorax, and wing covers become dark coffee brown with a tinge of green, darkest on the outer portion of the wing covers, lighter and slightly reddish dorsally. The abdomen is bright burnt sienna above, later changing to bright mahogany brown, with the posterior half of each segment darker than the anterior, and the cremaster much darker.

The darkening continues slowly through pupal life, the pupa becoming entirely blackish 2 or 3 days before the butterfly emerges.

For 2 or 3 days after the formation of the pupa the abdomen remains very flexible, and the pupa somewhat irritable. The abdomen then gradually shortens and toward the end of the pupal stage has become immobile.

When first formed the pupa is very shiny and has a wet appearance. With the darkening in color the appearance of wetness disappears, and a thin, even, finely granular lavender-gray bloom or pruinosity gradually begins to manifest itself. During the next 20 hours the bloom increases in density and extends itself all over the pupa, except for the narrow rings between the abdominal segments and the deepest portions of the sutures, appearing last on the wing covers, over which it spreads from the base to the tip. The outer portions of the wing covers are the last areas to be covered. Meanwhile all trace of green has disappeared from the pupa. The bloom now begins to lighten in color and to change from a granular to a flocculent appearance, transforming into a flocculent and rather thick covering, looking when magnified somewhat like light, flocculent lavender-tinted snow. It is absent from the soft bands between the abdominal segments and from the beveled edges of the latter, from the glazed eye, from the circular patches on the ventral side of the abdomen, from the deepest portions of the sutural lines, from the prothoracic and other spiracles, and from the cremaster, except the sunken ventral portion; but eventually it may spread over some or all of these, although the prothoracic spiracles and the cremaster are rarely more than lightly covered.

The bloom is of a soft waxy texture and forms a very efficient protection against water. It is only very slightly, if at all, soluble in alcohol.

In general form the pupa is most like that of *Achalarus lyciades*, with the abdomen plump and the anterior portion rather slender.

As viewed dorsally the head and prothorax form a subquadangular mass slightly broader in front than behind, nearly twice as broad as long, with very broadly rounded outer angles passing over into a rather strongly convex front of which the middle third has a convexity of its own that brings it very slightly in advance of the arc formed by

the two lateral thirds. The head is separated from the thorax by a narrow but rather deep suture. Toward the head and prothorax the sides of the mesothorax converge from the well-rounded basal wing tubercles at an angle of about  $30^{\circ}$  with the middorsal line, the straight converging portions of the sides of the mesothorax being about twice as long as the outer profile of the prothoracic spiracle.

When viewed from in front the head curiously suggests the head of a manatee.

The mesothorax is slightly broader than long, rather strongly and evenly convex, and very slightly broader posteriorly than anteriorly. The basal wing tubercles are low and broadly rounded.

As viewed dorsally, the body increases in width from the posterior end of the mesothorax to the third abdominal segment, then tapers at about the same rate gradually and evenly to the base of the cremaster.

The dorsal profile rises in a broad ellipse from the middle of the anterior end to the row of tubercles between the prothorax and mesothorax, then rises slowly in a broad curve to the end of the anterior third of the mesothorax, whence it runs in an almost straight line very slightly downward, descending somewhat abruptly near the end of the mesothorax, which rises in a slight convexity. From the end of the mesothorax the profile rises evenly and very slowly to the third abdominal segment, and the fourth which is nearly as high, then curves with increasing rapidity downward to the base of the cremaster.

From the middle of the anterior end the ventral profile curves in an ellipse to the basal portion of the antennae, then runs in an almost straight line to above the first abdominal segment, where it curves broadly and, reaching the maximum height above the third abdominal segment, descends in a more or less straight line to the base of the cremaster.

The prothoracic spiracles are large, auriculate with a protuberant flaring posterior lip, and are directed forward and very slightly outward. The outer side of the raised lip bears 12 to 14 broad, well-spaced rounded ridges that run from the base to the swollen and somewhat tubercular rim. Within the lip is a broad, dense band of short dark brown hairs attached to a curved semicircular shelf of nearly uniform width that leaves a large semicircular opening with a radius nearly or quite equal to twice the width of the band of hairs.

The position of the mandibles is indicated by a broad, low, rugose, hairless hump.

The maxillae reach very nearly to the tip of the wing covers.

The tip of the antennae is 3 mm from the end of the wing covers.

The posterior legs terminate 1 mm before the tip of the antennae, or at about the middle of the second abdominal segment.

The fore legs end 3 mm in advance of the hind legs.

The moveable abdominal segments are encircled just within the anterior end by a low, narrow, inconspicuous elevated band.

The cremaster is 2 mm long, slender and recurved, and bears on the truncate tip numerous slender light brown spines with the tips curved in varying degrees, sometimes in a spiral.

Except on the third and following abdominal segments, on the glazed eye, and sometimes on the antennae, the pupa is rather conspicuously sculptured.

On the mesothorax the sculpture is relatively inconspicuous, consisting of numerous more or less regular, fine transverse grooves and a fine median line.

On the outer thirds of the metathorax the sculpture consists of fine irregular diagonal grooves; the middle third is more coarsely sculptured.

On the first two abdominal segments the sculpture consists of fine, irregular transverse lines.

The prothorax is rather deeply sculptured with irregular deep transverse grooves in the two central quarters and laterally directed chevron-shaped grooves in the lateral quarters. Along the posterior border of the prothorax between the prothoracic spiracles there is a sharp tubercle about midway between the spiracle and the median line with usually one smaller one between it and the median line and two smaller ones between it and the spiracle.

The portion of the head between the epicranial suture and the prothorax is marked by a low triangle with its base on the epicranial suture, behind which are two wedges with their small ends joined in the median line. These latter bear fine longitudinal lines that toward the broader outer ends become chevron-shaped, with the angles directed inward; the outermost chevron has a few short transverse lines between it and the outer end of the segment. The rest of the head, except for the smooth glazed eye, is finely rugose with more or less wavy lines.

The ventral surface, except for the abdominal segments, is finely sculptured with mostly transverse lines. The antennae may be finely sculptured with irregular transverse lines, or may be quite smooth, showing only the segmentation.

The pupa is studded with long curved hairs which are most numerous about the head and on the dorsal portion of the thorax, becoming shorter, finer, and more scattered on the abdomen. On the head the

hairs are segregated into definite patches. There is a large patch on the front, a smaller patch on either side behind and outside of this, just within the anterior portion of the base of the antennae, a large patch on the sculptured portion of the eye, a smaller patch beyond this and separated from it by the glazed eye, and a small but conspicuous patch on either side of the labrum.

There are no hairs on the wing covers or elsewhere on the ventral surface, except as follows. The first abdominal segment beyond the wing covers ventrally bears on either side of the median line a row of three hairs, the outermost the longest, at some distance beyond this a single hair, almost as far again beyond this single hair a group of three hairs arranged in a triangle, and beyond these seven widely scattered hairs. The next segment has the hairs similarly arranged. The segment following has the innermost group reduced to two hairs, and three hairs arranged in an equilateral triangle in place of the single hair on the segments preceding. The next segment has one hair anteriorly and near the median line, another slightly behind and outside this, two more beneath the middle of the space between the inner two hairs and the group of three on the preceding segment, and several more near the outer border. The segment preceding the cremaster has two hairs, one in front of the other, beneath the two innermost hairs on the preceding segment, and several more hairs in the outer portion of the posterior half.

The cremaster is provided with numerous long, stout hooks with the tips recurved spirally so that the point is on one side of and some distance from the shaft.

Eight pupae give the following dimensions:

Length mm	Maximum width mm	Minimum width mm	Width of head mm
20.5	6.2	5.5	4.5
17.3	6.4	5.0	4.3
17.5	6.3	4.8	4.0
18.2	6.2	4.8	4.0
17.7	6.4	5.0	4.0
16.8	6.0	4.7	4.1
17.7	6.4	5.2	4.0
18.0	6.8	5.7	4.2
—	—	—	—
Average 17.9	6.3	5.1	4.1

These measurements were made from pupae formed by caterpillars in captivity. As the caterpillars were not fed it is possible that the pupae are slightly below the average size. However, normal-sized butterflies emerged from others of the same lot.



When the butterfly emerges, the pupa splits first along the suture running between the posterior ends of the bases of the antennal sheaths, then along the inner edge of the antennal sheaths, and finally down the middle of the thorax dorsally. Three pupae were broken open in the same way.

In *Epargyreus tityrus* the escape of the butterfly is made after the same fashion, except that the second rupture is down the outer side of the antennal sheath instead of down the inner side. Thus in empty pupal cases of *Rhabdoides cellus* the antennal sheaths remain attached to the inner edges of the wing cases, whereas in empty pupal cases of *Epargyreus tityrus* they remain attached to the midtibial sheaths.

#### PARASITE

From one of the caterpillars a tachinid larva emerged and immediately pupated. In a few days the adult emerged from the pupa. Charles T. Greene was so kind as to identify this for us. It proved to be an example of *Achaetoneura aletiae* (Riley).

#### KEY TO THE EGGS OF RHABDOIDES AND RELATED GENERA

- $a^1$ . Egg regularly domed above, with no portion truncate; vertical ribs at least 15 (15 to 21) in number.
  - $b^1$ . Vertical ribs very fine and low, becoming higher and conspicuously beaded above the middle of the egg; a broad area about the micropylar basin occupied by a large meshed and conspicuous reticulation in which the ribs and the widely spaced cross lines are smooth and of the same height and character.
    - $c^1$ . With 15 to 21 (usually 17 or 18) vertical ribs; egg nearly as high as broad ..... *Rhabdoides*.
    - $c^2$ . With about 15 vertical ribs; egg a fourth broader than high.
      - Thorybes*.
  - $b^2$ . Vertical ribs high and conspicuous, not increasing in height above the middle of the egg; alternate ribs run to the micropylar basin; no conspicuous reticulation about the micropylar basin, the ribs and fine cross lines continuing directly to it..... *Epargyreus*.
- $a^2$ . Egg broadly truncate above over an area about equal in diameter to half the width of the egg; vertical ribs not over 15 in number.
  - $b^1$ . With at most 12 vertical ribs; egg one-eighth again as broad as high.
    - Goniurus*.
  - $b^2$ . With more than 12 vertical ribs; egg one-fourth again as broad as high ..... *Achalarus*.



KEY TO THE CATERPILLAR AT BIRTH IN RHABDOIDES AND  
RELATED GENERA

- a*<sup>1</sup>. Head excessively large; dorsal shield of first thoracic segment conspicuous; first pair of thoracic legs conspicuously more corneous than the others; head orbicular.
  - b*<sup>1</sup>. First thoracic segment with only the dorsal shield corneous.
    - c*<sup>1</sup>. Dorsal shield of first thoracic segment not nearly reaching the spiracles on either side.
      - d*<sup>1</sup>. Head light brownish yellow; dorsal shield of first thoracic segment much darker; body chrome yellow.....*Rhabdoides*.
      - d*<sup>2</sup>. Head black, sometimes blackish brown; dorsal shield of first thoracic segment of the same color as the head; body uniform pale yellow .....*Goniurus*.
    - c*<sup>2</sup>. Dorsal shield of first thoracic segment reaching and including the spiracles on the side.....*Achalarus*.
  - b*<sup>2</sup>. First thoracic segment entirely corneous.....*Thorybes*.
- a*<sup>2</sup>. Head only moderately large; dorsal shield of first thoracic segment inconspicuous; all the thoracic legs alike in texture; head subpyramidal, much narrower above than below.....*Epargyreus*.

KEY TO THE MATURE CATERPILLAR IN RHABDOIDES AND RELATED  
GENERA

- a*<sup>1</sup>. Papillae of body inconspicuous, except by their color.
  - b*<sup>1</sup>. With a conspicuous bright-colored lateral stripe, the transverse markings in dots only.
    - c*<sup>1</sup>. Prolegs and end of body of the same color as the rest of the body, but paler; first thoracic segment as far as the dorsal shield bright rose pink .....*Rhabdoides*.
    - c*<sup>2</sup>. Prolegs orange, with blackish fuscous claws; end of body orange; first thoracic segment as far as the dorsal shield reddish..*Goniurus*.
  - b*<sup>2</sup>. Markings wholly transverse and in broken lines, the longitudinal markings being wholly interrupted.....*Epargyreus*.
- a*<sup>2</sup>. Papillae of body conspicuous, giving it a granulated appearance.
  - b*<sup>1</sup>. Collar half as broad as the head.....*Achalarus*.
  - b*<sup>2</sup>. Collar distinctly less than half as broad as the head.....*Thorybes*.

EXPLANATION OF PLATES

PLATE I (FRONTISPIECE)

Early stages of *Rhabdoides cellus* (inset, right center). *Left*: Full-grown caterpillar removed from its shelter. *Left center*: Fourth-stage caterpillar. *Just beneath the preceding*: A shelter or tent made by a third-stage caterpillar. *Upper, left side*: A leaf with three tents made by a first-stage caterpillar about one-twelfth of an inch long. *Lower right, beneath the petiole of the leaf*: The very inconspicuous shelter made by a full-grown caterpillar. *Upper right*: A string of five eggs attached to the under surface of a leaf. *Inset, lower left*: A pupa, removed from the cocoon. Painting by Hashime Murayama. The caterpillars are from color sketches of living specimens by Dr. Doris M. Cochran. Reproduced by courtesy of the National Geographic Magazine.

## PLATE 2

- FIGS. 1, 2. Variety *leilae*, type specimen, raised from a caterpillar from near Great Falls, Md., emerged July 20, 1934, upper (1) and under (2) sides. U.S.N.M. no. 51415.
- FIGS. 3, 4. A specimen from near Great Falls, Md., June 3, 1934, upper (3) and under (4) sides.
- FIGS. 5, 6. A specimen from near Great Falls, Md., June 10, 1934, upper (5) and under (6) sides.
- FIGS. 7, 8. A specimen from Charleston, W. Va., May 22, 1900, upper (7) and under (8) sides.

## PLATE 3

- FIGS. 9, 10. A specimen from Tallahassee, Fla., collected by Albert Koebele, upper (9) and under (10) sides.
- FIGS. 11, 12. A specimen from Palmerlee, Ariz., upper (11) and (12) under sides.
- FIGS. 13, 14. A specimen from Lititz, Pa., collected by J. J. Heiserman, July 16, upper (13) and under (14) sides.

## PLATE 4

- FIGS. 15, 16. A specimen from Volcan Santa Maria, Guatemala, collected by William Schaus and John Barnes in June, upper (15) and under (16) sides.
- FIG. 17. A string of five eggs, of which the first and fourth are slightly chipped and contain dead larvae.  $\times 5$ .
- FIG. 18. A rent in a leaf forming one side of a cocoon which has been repaired by the caterpillar.

## PLATE 5

Pupae of *Rhabdoides cellus* and *Epargyreus tityrus*.

All figures  $\times 2$ .

- FIG. 19. *Rhabdoides cellus*, living pupa, lateral view.
- FIG. 20. The same pupa, ventral view.
- FIG. 21. Another living pupa, dorsal view.
- FIG. 22. The same pupa, lateral view.
- FIG. 23. *Rhabdoides cellus*, a pupa with the wax removed, lateral view.
- FIG. 24. The same pupa, ventral view.
- FIG. 25. Another pupa, dorsal view.
- FIG. 26. *Epargyreus tityrus*, a small pupa, lateral view.
- FIG. 27. The same pupa, ventral view.

## PLATE 6

- FIG. 28. An egg, slightly chipped about the apex and containing a dead larva.  $\times 17$ .
- FIG. 29. Three empty egg shells.  $\times 17$ .
- FIG. 30. Two caterpillars just from the egg.  $\times 12$ .

- FIG. 31. Two caterpillars in the second stage.  $\times 12$ .  
FIG. 32. Three caterpillars in the second stage.  $\times 2.5$ .  
FIG. 33. A caterpillar in the third stage.  $\times 2.5$ .  
FIG. 34. Four caterpillars in the fourth stage.  $\times 2.5$ .  
FIG. 35. Three caterpillars in the fifth (last) stage.  $\times 2.5$ .  
FIG. 36. Head of full-grown caterpillar.  $\times 2.5$ .

*Note.*—The photographs of caterpillars are from specimens in alcohol that have lost their markings; but the uppermost last stage caterpillar shows the light dorsolateral line fairly well.

#### PLATE 7

(All figures natural size.)

- FIG. 37. Shelter of a third-stage caterpillar.  
FIG. 38. The same, in side view.  
FIG. 39. The same, in end view.  
FIG. 40. Diagram illustrating the construction of the shelter; the portion of the leaf between the cuts is bent inward over the upper surface, the angles following the direction of the dotted lines to the arrow points; in this case the vein of the leaf forms a sort of ridge pole for the shelter.  
FIG. 41. Two first-stage shelters.  
FIG. 42. The same leaf in edge view, showing the elevation of the shelters.

#### PLATE 8

- FIG. 43. Caterpillar at birth.  
FIG. 44. A circlet of crochet tips on the proleg of a full-grown caterpillar.  
FIG. 45. A section of the band of crochets, viewed exteriorly; the recurved tips are shown in black.  
FIG. 46. Crochets of the three series, in side view.  
FIG. 47. First thoracic segment of a full-grown caterpillar.  
FIG. 48. Head and first thoracic segment of a full-grown caterpillar, dorsal view.  
FIG. 49. Head capsule of a first-stage caterpillar, front view.  
FIG. 50. The same, rear view.  
FIG. 51. Jaw of a full-grown caterpillar.  
FIG. 52. Anal structures of a full-grown caterpillar.



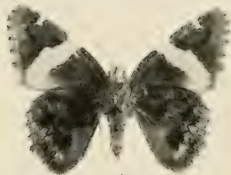
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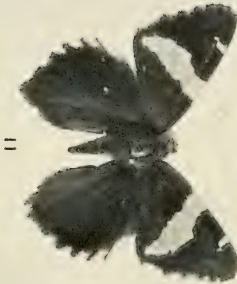
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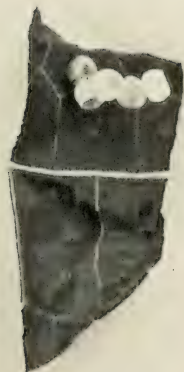
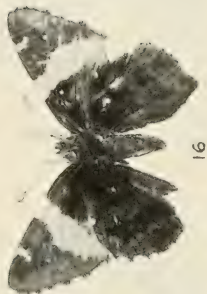
**RHABDOIDES CELLUS FROM VARIOUS LOCALITIES**

(For explanation, see p. 49.)



RHABDOIDES CELLUS FROM VARIOUS LOCALITIES

(For explanation, see p. 49.)

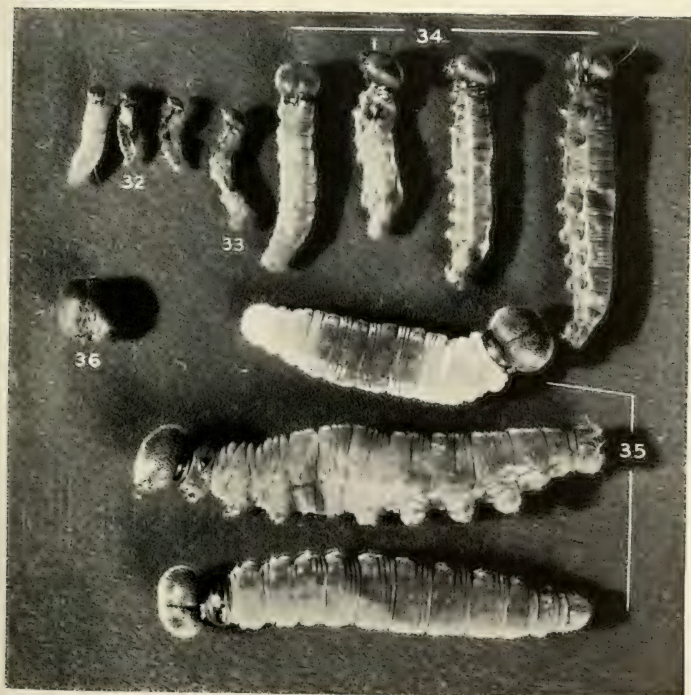
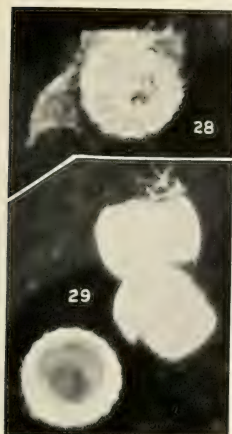


**RHABDOIDES CELLUS (GUATEMALA), EGG STRING, AND PATCHED LEAF**  
(For explanation, see p. 49.)



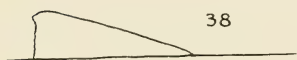


PUPAE OF RHABDOIDES CELLUS AND EPARGYREUS TITYRUS  
(For explanation, see p. 49.)

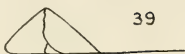


EGGS AND LARVAE OF RHABDOIDES CELLUS

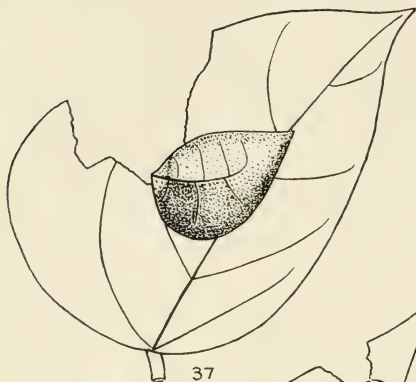
(For explanation, see pp. 40, 50.)



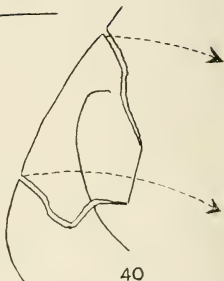
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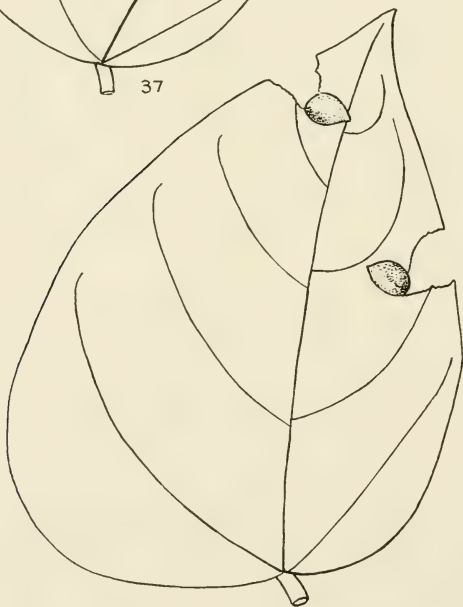
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SHELTERS MADE BY LARVAE OF RHABDOIDES CELLUS  
(For explanation, see p. 50.)



43



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47



48



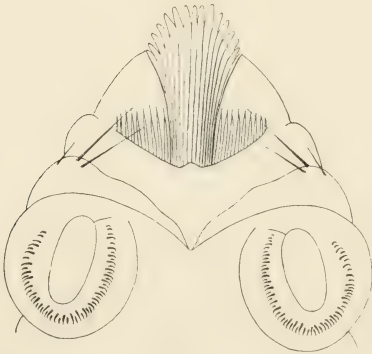
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52

DETAILS OF LARVAE OF RHABDOIDES CELLUS

(For explanation, see p. 50.)



SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 95, NUMBER 8

# THOMAS WALTER, BOTANIST

BY  
WILLIAM R. MAXON  
U. S. National Museum



(PUBLICATION 3388)

CITY OF WASHINGTON  
PUBLISHED BY THE SMITHSONIAN INSTITUTION  
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## THOMAS WALTER, BOTANIST

By WILLIAM R. MAXON

*U. S. National Museum*

The first descriptive treatise upon the flowering plants of any definite region in eastern North America, using the binomial system of nomenclature, is the "Flora Caroliniana" of Thomas Walter, published at London in 1788 by the famous botanical collector John Fraser, at the latter's expense. This important and historically interesting volume, the specimens upon which it is based, Walter's botanical activity in South Carolina, and visits by more than one eminent botanist to his secluded grave on the banks of the Santee River have been the subjects of several articles, yet comparatively little is known about the man himself. The present notice is written partly with the purpose of bringing together scattered source references, correcting an unusual and long-standing error as to the date of Walter's death, and furnishing data recently obtained as to his marriages, and partly in the hope that something may still be discovered as to his extraction, education, and early life and the circumstances of his removal to this country. For the sake of clearness and both general and local interest these points may be dealt with somewhat categorically.

*Birth and education.*—Walter was a native of Hampshire, England, and is known merely to have emigrated "as a young man" to South Carolina, where he acquired a plantation on the banks of the Santee River and passed the remainder of his short life. The date of his birth has been placed doubtfully at 1740. That he was a man of very considerable education is obvious from the text of his book, which throughout is written in classical Latin, from the character of his few letters, and from the testimony of his warm friend, Fraser.

*His home on the Santee.*—The Walter plantation lay at the southern edge of the great swamp bordering the Santee River, in the coastal plain. Its location is given sometimes (probably with correctness) as in St. John's Parish, sometimes as in St. Stephen's, but in any case it is within the boundary of present-day Berkeley County. The date of its acquisition is not known, nor whether it was obtained by purchase or by original grant. Here, in this prosperous region so well described by Coker, he lived during the Revolutionary period and its turbulent

internecine local warfare the life of a gentleman farmer, botany being at least an absorbing avocation. Porcher states that Walter's "devotion to the cause of science led him to the wilds of Carolina", and it is not difficult for us to accept this as a motive, in spite of the doubts implied by Britten. It explains his assiduous study of the flora of the region, his painstaking analysis of a majority of the species sought out, his laborious preparation (completely isolated though he was) of an erudite "flora" of the region, and the formation of a veritable botanical garden upon his estate, where he is said to have brought into cultivation, aside from exotics, a majority of the species described in his book. According to Coker the plantation became after Walter's death a part of the estate called Mexico and for a long time was owned by the Porcher family.

*Marriage and descendants.*—Walter was thrice married, the essential data being as follows:

(1) March 26, 1769, apparently while residing in Charleston, to Miss Anne Lesesne, of Daniels Island,<sup>1</sup> who died September 11 of the same year.<sup>2</sup> These published data are substantiated by Miss Anne A. Porcher, of Pinopolis, South Carolina, a great-great-granddaughter of Walter, from records entered in the family Bible.

(2) March 20, 1777, to Miss Ann (not Sarah) Peyre, born March 26, 1755, the fourth child of Samuel Peyre and Sarah (Cantey) Peyre. According to the published record<sup>3</sup> their issue was as follows: (i) Ann Walter, married May 29, 1794, to Thomas Hasell Thomas, of St. Stephen's Parish, died April 25, 1818; (ii) Mary Peyre Walter, born in 1780, married August 19, 1800, to Francis Peyre, her cousin, died January 4, 1818. This record is supplemented by Miss Anne A. Porcher to the effect that Ann (Nancy) was one of twins born in 1777, her sister (Polly) dying in October 1779, and that Mary Peyre Walter was born December 5, 1780, her mother dying in childbirth.

(3) Date unknown, to Miss Dorothy (Dolly) Cooper, concerning whom nothing apparently is of record. Their daughter, Emily, married Judge Thomas Usher Pulaski Charlton.

The record of Walter's numerous descendants was sketched by Coker in 1910, at which time some of the above data apparently had not been published, the fact of Walter's earliest marriage being unmentioned. He refers to a son, Thomas, born of the Peyre marriage, who reached maturity but died (unmarried) before his father. No record of this son has been found by Miss Porcher.

<sup>1</sup> So. Car. Hist. & Gen. Mag. 11: 37. 1910.

<sup>2</sup> Ibid. 10: 157. 1909; 16: 91. 1915.

<sup>3</sup> Ibid. 11: 221, 222, 241. 1910.

*Death and burial.*—Walter died January 17, 1789, "of fever", according to Fraser, or on January 18, 1789, according to Sylvanus Urban. Nevertheless, James Britten gives the year as 1788 in his extended notice, "Thomas Walter (1740?-88) and his Grass", though accepting from Fraser the month, January, and at the same time quoting freely from two letters which, as he correctly states, were written by Walter to Fraser from the Santee on February 18, 1788, and October 9, 1788! These letters are published in full by Fraser. Britten's error has apparently passed unnoticed by all save Dr. John Hendley Barnhart (1928). It is not typographical, but is an odd inadvertence on the part of one well known for meticulous accuracy in biographic and bibliographic detail, and is presumably due to Britten's having unconsciously accepted the erroneous date inscribed upon Walter's tombstone, now to be mentioned.

At his own request Walter was buried on the Santee plantation. His grave was visited by Ravenel in 1856, by Brainerd in 1907, and by Coker in 1910, all of whom published interesting accounts of the region, the gradual reversion of the estate to forest, and the consequent complete neglect of the grave. Each quoted also the inscription upon the tombstone, which is a slab of white crystalline marble about 6 feet long, 2 feet 8 inches broad, and 2 inches thick. According to Brainerd the wording (with a single minor correction) is as follows:

In memory of Thomas Walter. A native of Hampshire in England and many years a resident of this State. He died in the beginning of the year 1788. Aetatis cir. 48 ann. To a mind liberally endowed by nature and refined by a liberal education he added a taste for the study of Natural History and in the department of Botany science is much indebted to his labours. At his desire he was buried in this spot, once the garden in which were cultivated most of the Plants of his FLORA CAROLINIANA. From motives of filial affection his only surviving Children ANN and MARY have placed this memorial.

This inscription, according to family records, was written by the South Carolina botanist, James Macbride, who died in 1817. The phrase "his only surviving children", if true, indicates that the monument must have been erected many years after Walter's death, since Emily Walter (Charlton), born of his third marriage, lived to bear three children, two of whom (sons) survived and left numerous progeny.<sup>4</sup> The error, 1788 for 1789, is thus explainable; nevertheless the erroneous inscribed date naturally found general acceptance.

<sup>4</sup> Further corroborative evidence is found in the signature below the inscription. According to Miss Porcher this, although the letters are worn, is definitely not "J. H. D.", as given by Brainerd, but "J. Hall." J. Hall was a stonecutter of Charleston, who erected a number of stones in the vicinity, "all around 1812-1816."



It may here be noted that Walter's grave, after its neglect for more than a hundred years, has recently (1931) been put in order. According to H. R. Dwight, of Pinopolis, it "has been completely restored, with new brick and cement foundation, and the slab repaired and replaced, and a handsome wrought iron fence, 15 ft. square, with gate, has been placed around it." An excellent photograph substantiates this. Mr. Dwight has very kindly sent me also a copy of the inscription upon a bronze tablet to Walter recently erected on State Highway no. 45, at a point where the road to the grave, 3 miles away, branches off.

*Flora Caroliniana*.—Walter's "Flora" is an octavo volume of 263 pages (exclusive of title page, dedication, preface, and index), describing upward of 1,000 species distributed among 435 genera. Of the former, more than 200 are described as new; of the latter, 32 are so indicated, but only 4 of these are given distinctive names. The work is classical and well deserves the attention it has received. It is based upon studies of specimens collected by Walter within a radius of 50 miles from his plantation and upon similar material brought him by Fraser, who, according to his own account, landed at Charleston September 20, 1786, and "having resided in South Carolina and Georgia nineteen months \* \* \* returned to England in the month of March, 1788." (Fraser's arrival in South Carolina is commonly dated 1785, in error.) The preface of the "Flora" bears the date 30 Dec. 1787. Fraser took the manuscript to England and published it in 1788, as previously stated. Concerning his own travels and the sources of Walter's material he writes most interestingly in the rare folio volume to which reference is here repeatedly made.

Along with Walter's manuscript Fraser carried to England "upwards of thirty thousand dried specimens of plants" of his own collecting and, what is of greater importance to us, the Walter herbarium. The Herbarium remained in the hands of the Fraser family until 1849, when (May 23) it was presented to the Linnean Society of London "by John Fraser, son of John Fraser, the indefatigable North American Botanical Collector from the years 1786 to 1811." It was purchased by the British Museum (Natural History) in 1863, at a sale of the Linnean Society's "surplus collections", for the small sum of 15 shillings. Upon Asa Gray's inquiry during his first visit to England (1839) it had been found in the possession of John Fraser 2d and was submitted to Gray for study. It has been examined more or less critically by many later American botanists, a number of whom are listed by Britten. The grasses have been discussed by Hitchcock. But unfortunately the herbarium is in poor condition and must have

consisted originally of meager specimens, so that its value in the interpretation of Walter's short descriptions is often slight. Various details as to its labeling and condition, the absence of certain specimens (including many types), the identification of Walter's own species, and his interpretation of earlier species are given by Blake, whose paper is commented upon by Britten.

*Fraser's Carolina Grass*.—This grass, the subject of Fraser's important folio, is *Agrostis perennans* (Walter) Tuckerman, now known as "autumn bent", a widely distributed species of eastern North America. The commercial venture entered into by Walter and Fraser of introducing this into general cultivation in England ended disastrously, and was cut short by Walter's death.

*Data sought*.—Aside from such information as date and place of birth, education, early history, dates of arrival in South Carolina and acquisition of plantation, and the like, all of this unrecorded, it is desirable surely to know something more of Walter's life in this country and of the man himself than can be gained from his single publication, the two letters quoted by Fraser, and the latter's warm eulogy of his friend, whom he knew for so short a time. Dignity, scholarship, conservatism yet independence of judgment, and—above all—modesty and persistent zeal are so unmistakably reflected in the lines of his preface to the "Flora" that one earnestly hopes that diaries, letters, or contemporaneous accounts or records of some sort may yet be found, which will shed real light upon the life history of this gifted scientist. Why should he have sought seclusion on the Santee? Miss Porcher writes (February 19, 1936): "Evidently Walter remained an Englishman to his death. In our family, whenever he was spoken of, the fact that he was never naturalized was always stressed. His brothers-in-law, the Peyres, remained Loyalists and were both put in prison in Philadelphia." Only one signature of Thomas Walter is known to exist, this in receipt of a bill of goods (September 28, 1787) amounting to 115 pounds, 11 shillings, 4 pence.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS

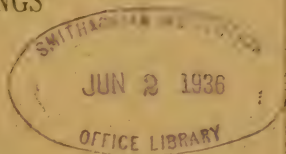
VOLUME 95, NUMBER 9

PRELIMINARY OBSERVATIONS ON GROWTH  
AND PHOTOTROPIC RESPONSE OF  
OAT SEEDLINGS

BY

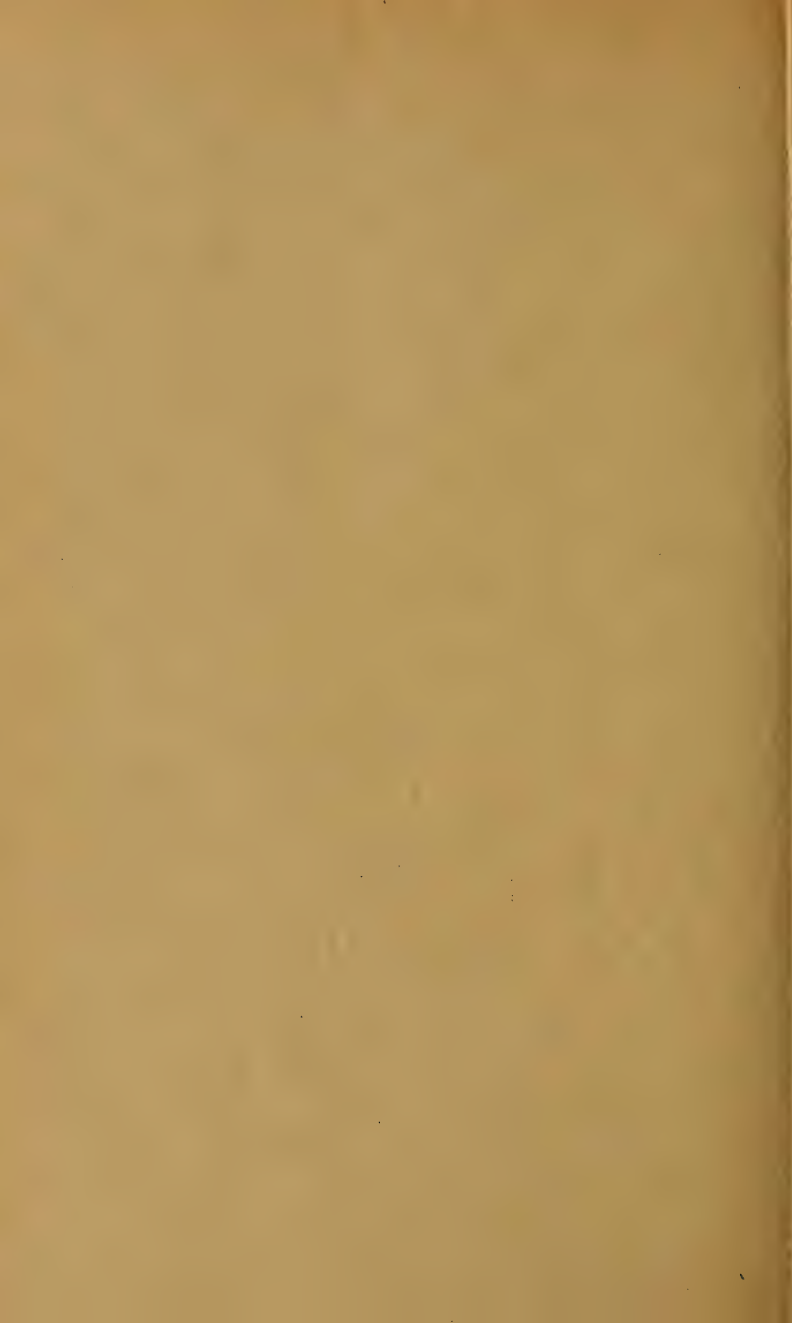
ENOCH KARRER

Division of Radiation and Organisms  
Smithsonian Institution



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## PRELIMINARY OBSERVATIONS ON GROWTH AND PHOTOTROPIC RESPONSE OF OAT SEEDLINGS

By ENOCH KARRER

*Division of Radiation and Organisms, Smithsonian Institution*

If oat seedlings are germinated while exposed to the continuous spectrum, the shoots in the blue region will curve toward the light source. This bending out of the plane of the spectrum is the ordinary phototropic response. In addition there appears to be a bending within the plane of the spectrum. The curvature in the blue just mentioned has components in the plane of the spectrum such that the tips of the seedlings converge. In the deep red, seedlings do not converge as in the blue, but diverge in the plane of the spectrum. In this region there is no bending out of the plane of the spectrum. There is no ordinary phototropic sensitivity (1)<sup>1</sup> in this region.

The components of curvature in the spectral plane seem not to be an effect of intensity gradient, but rather of a wave-length gradient, for the convergence and divergence occur on both sides of a particular narrow spectral region. It might also be the effect of a concentration gradient of a substance emanating from the seedlings. Such substances must themselves be products resulting from the effects of the radiation. The convergence occurs in the region of wave length 4,750. The divergence occurs in the region of wave length about 6,220.

As for other types of spectral response: the greatest elongational growth was in this blue region of convergence, and the next greatest in this red region of divergence. The greenest growth was in the region from 5,910 to 6,130; the yellowest from 4,356 to 5,200. Roots were longest in the extreme blue (4,356-4,800), and shortest beyond 6,200. The leaf sheath (the coleoptile) was most filled out by the first leaf in the green and orange; least filled out in the blue and deepest red regions. In the green region there appeared to be stunted growth of the coleoptile and the inner leaf broke through prematurely, but later growth in white light of seedling taken from this region was rapid. In the green, and at certain places toward the red, there appeared to be evidence of negative phototropism involving only the extreme tip of the coleoptile.

The spectrum utilized was obtained from a concave grating. The wave-length intervals throughout the spectrum are uniform. The

<sup>1</sup> Numbers in parentheses refer to list of literature cited at end of paper.

grating was not of the highest quality, but precautions against spurious effects from scattered light were taken by employing filters of colored cellophane.

Although the idea of forces arising from a wave-length gradient may appear strange, they are to be predicted under certain conditions. There are many varied functions performed in and by various parts of the plant. In respiratory processes, carbohydrates, fats, and proteins, water and minerals are mobilized and oxidized. In synthesis, in addition to the simple process of carbohydrate formation, there are reactions with ammonia or other nitrogen compounds, and further condensation and polymerization of the synthesized products. Also

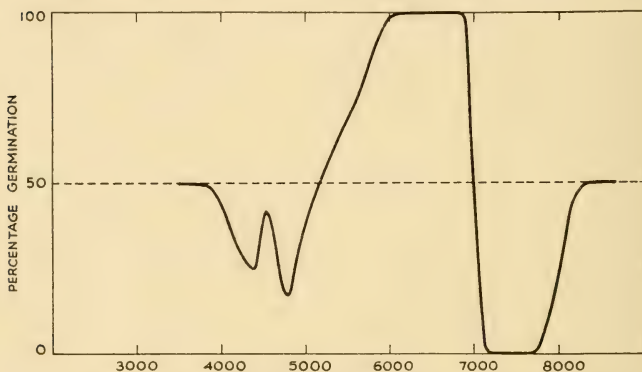


FIG. 1.—The percentage of germination (ordinates) of light-sensitive lettuce seed in different wave-length regions (abscissae) of the spectrum after an exposure to red light sufficient to effect a 50 percent germination. (From Flint and McAlister.)

the processes of transportation and storage are involved. Many different enzymes, catalysts, and hormones must be involved. Some of the processes other than the simple carbohydrate synthesis that is ordinarily thought of in connection with photosynthesis must involve external energy obtainable by thermal contact or from radiant energy of effective wave length.

Recently the effect on the germination of lettuce seed of radiant energy of various frequencies has been determined by Flint and McAlister (2). They found regions of inhibition and of activation in the spectrum of the light of the incandescent tungsten filament. The significant point is that the boundary between promoting and inhibiting regions is very sharp. (See figure 1.) If a light source had

been used in which the energy in shorter wave lengths was equal to that of the longer, the steepness of slope would probably be greater on the blueward side than the curve indicates. One might expect that the seeds placed at these sharp wave-length boundaries would experience greatly different forces at various parts of their structure. If the differential action is at all translated into mechanical effects, phenomena such as the divergence and convergence noted above or twisting may be expected.

Another photic effect was observed in seeds which, after having been soaked several hours in nutrient solution, were exposed for a short time to an elevated temperature. They germinate to different extents and grow at different rates. Wet seeds exposed for 3 minutes to 40° C. are accelerated in the germinational growth, but a smaller percentage of seeds may germinate. The marked effect of exposure to 40° C. may be conditioned by the hydrolysis of starch which is promoted at that temperature (3). The effect of heating on dormancy of seeds is well known. However, if in addition to heating at different temperatures the seeds be irradiated in different parts of the spectrum, they appear to be differently sensitized to different wave lengths. Seeds subjected to the higher temperatures appeared to have greatest percentage germination in the blue, as though they were more and more dependent for germination on the blue. These are preliminary observations, but, like the photic effect first mentioned, are suggestive of a line of experimentation.

All the observations were begun at room temperatures (variable from 20° to 28° C.). Some tests for optimum temperature were initiated. Four batches of seeds, after soaking for several hours on filter paper in closed aluminum cups, were exposed for 3 minutes to 40° C. Three batches were not exposed. One of each set was kept at 25° (call these f25 and c25). Another of each was kept at 20° (call these f20 and c20). One from each set was alternated between 25° and 20° C. (f25/20, c25/20), and one (f40/20) of the first set was alternated between 20° and 40° C., being exposed twice every day for 3 minutes to a temperature of 40° C.

The longest roots and shoots, but most spindly, were in f25 (those exposed 3 minutes to 40° and kept at 25°). Next longest were in c25/20. These two also had lowest root and shoot ratio (1.2). The lowest percentage (25 per cent) of germination was in c25/20. The shortest roots and shoots were in f20/40; but greatest root shoot ratio (4.2), most hair roots, and thickest coleoptiles.

The next to the most hair roots were in f20; next to thickest coleoptiles in f25/20. Greatest percentage (76.4) germination was in f25/20.

The most growth by weight of roots and shoots of all seedlings occurred in f25/20 (15.9) and in c25/20 (14.5); least growth by weight (4.4) in f20/40; next to lowest, f25 (7.1).

All seeds were germinated in contact with nutrient solution (4), for it was found that roots function immediately as they form; and in their functioning affect immediately the growth of the seedlings with the materials they chance to meet.

The above observations were made on several occasions incidental to a study of the optimum conditions for obtaining coleoptiles of uniform reactivity phototropically. They are more a contribution to the discussion of the subject of standardization of the conditions of growth in plant physiology than announcement of new phenomena established. This study has been interrupted and the critical repetition of the observations for the time being intercepted.

The experiments, though incomplete, have led me to the following conclusion: that the conditions for optimum growth and for greater uniformity of phototropic response involve (1) contact with nutrient solution; (2) radiant energy of extended wave lengths—at least different wave lengths at different stages of growth; (3) a wave of temperature rather than constant temperature; (4) perhaps darkness as well as light; and (5) proper atmosphere.

I express appreciation to Secretary C. G. Abbot for the facilities and opportunity placed at my disposal to carry on this work, to Dr. E. S. Johnston, assistant director of the Division of Radiation and Organisms of the Smithsonian Institution, and to members of the Staff of the Division.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 10

# ADDITIONAL INFORMATION ON THE FOLSOM COMPLEX

REPORT ON THE SECOND SEASON'S INVESTI-  
GATIONS AT THE LINDENMEIER SITE  
IN NORTHERN COLORADO

(WITH 12 PLATES)

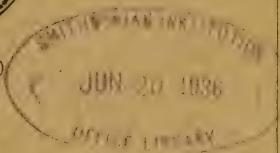
BY

FRANK H. H. ROBERTS, JR.

Archeologist, Bureau of American Ethnology



(PUBLICATION 3390)



CITY OF WASHINGTON  
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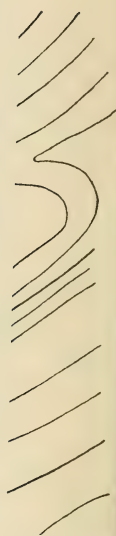
### MAP

Map 1. The Lindenmeier site.....	(Frontispiece)
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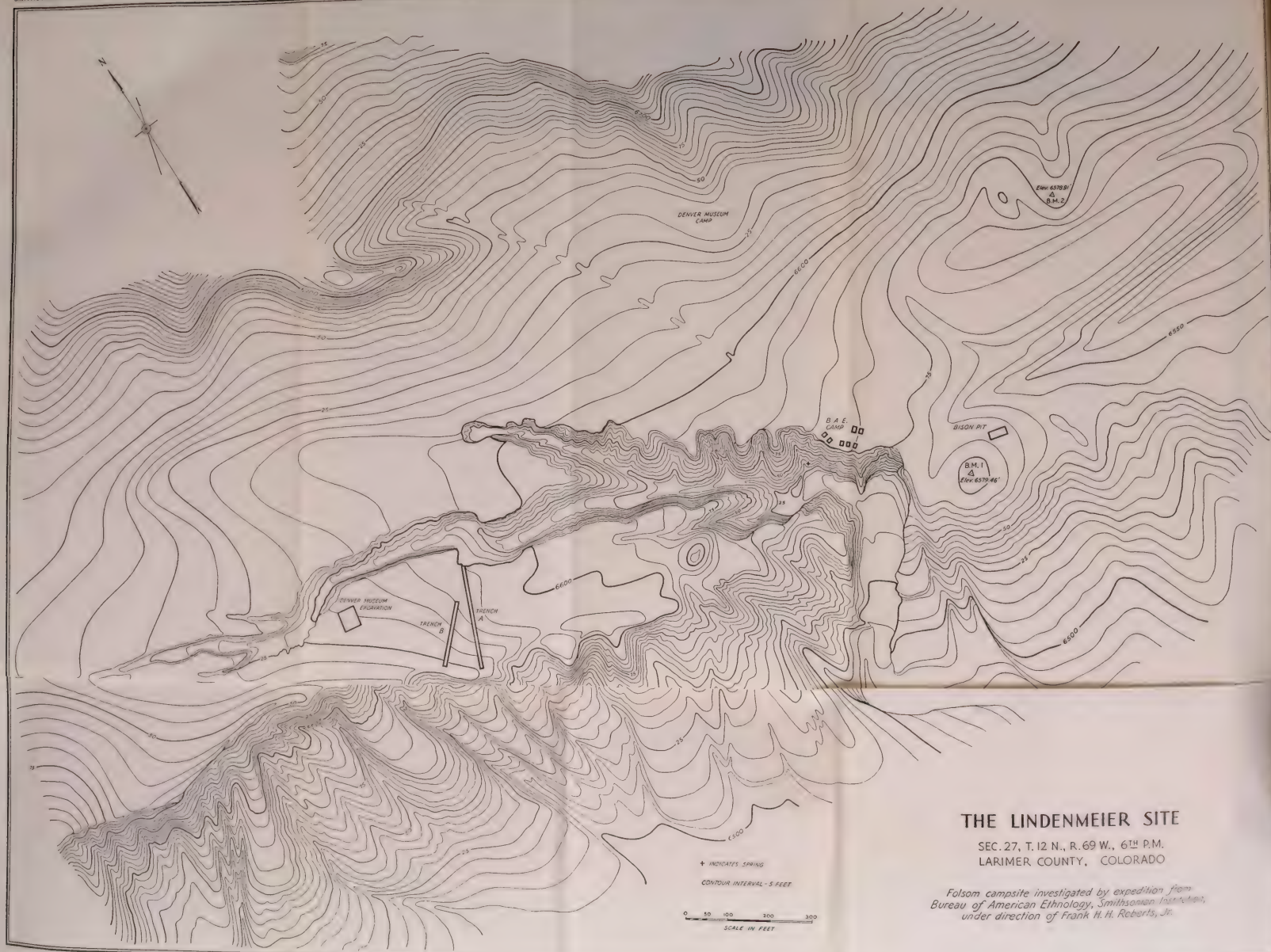
#### INTRODUCTION

During the summer of 1935 further investigations were conducted at the Lindenmeier site in northern Colorado. It was at this location that the first definite complex of stone implements attributable to Folsom man was found in situ in the autumn of 1934.<sup>1</sup> From the first of June until early September the writer and a group of associates carried on a series of excavations in an effort to obtain more information on this little-known phase of American archeology. The results were gratifying in some respects but in others fell short of expectations. The digging yielded 750 artifacts, large quantities of chipper's debris—immense fragments of stone forming a byproduct of the tool-making industry—and several deposits of bones from animals whose flesh or skins had been used by the one-time dwellers at the site. No human skeletal material was found. This was disappointing, inasmuch as all interested in the subject are anxious to know what the people are like who made the implements. Fragments of charcoal and scattered ashes were plentiful, but no indications of a shelter or habitation were observed. The presence of hammerstones accompanied by chips and flakes was noted at a number of places. These suggested that one or more individuals had been seated there while shaping tools out of rough stone nodules. Pieces of several projectile points, as well as other implements, that had been broken in the making were obtained from one such spot. By fitting the fragments together and restoring the flakes it is possible to gain good evidence concerning the technique used in manufacturing the tools.

Dr. Kirk Bryan, of the division of geology, Harvard University, assisted by Franklin McCann and John T. Hack, spent the month of

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<sup>1</sup> Roberts, 1935.





July in studying the geology of the district. As a part of their investigations they prepared a map of a portion of the terrain lying to the east of the archeological site. To facilitate their work, a level was run from a United States Geological Survey bench-mark (located on the line between sec. 19, T. 12 N., R. 68 W., and sec. 24, T. 12 N., R. 69 W., sixth principal meridian) and an accurate bench-mark based on mean sea level datum established at the site. E. G. Cassedy, illustrator for the Bureau of American Ethnology, joined the party in August and made a survey of the site proper, and some of the outlying area not mapped by Bryan. Mr. Cassedy has combined his and Bryan's surveys in a map showing the general topographical features of the site and adjacent region.

The announcement of the finds made at the Lindenmeier site in the autumn of 1934 attracted wide-spread attention and aroused a lively interest in the subject. As a result there were many visitors while work was under way. The numerous groups included anthropologists, paleontologists, geologists, geographers, and various scientists whose fields of research are not closely related to the present investigations. Among the anthropologists attracted to the site during the summer of 1935 were: A. V. Kidder and E. H. Morris, of the Carnegie Institution of Washington; E. W. Haury and E. B. Sayles, of Gila Pueblo, Globe, Ariz.; Donald Scott, of the Peabody Museum, Cambridge, Mass.; L. L. Leh, of the Department of Anthropology, University of Colorado; R. L. Zingg, of the University of Colorado Summer School, and his class in anthropology. Dr. E. B. Renaud, of the University of Denver, visited the site a number of times prior to 1935, and W. D. Strong, of the Bureau of American Ethnology, spent 2 days there while the writer was at work in the autumn of 1934. Geologists, paleontologists, and geographers present during the summer were: Paul MacClintock, Princeton University; Frederic B. Loomis, Amherst College; Wm. Van Royen and A. L. Lugin, University of Nebraska; C. Bertrand Schultz, of the Nebraska State Museum.

Members of the party engaged in the actual archeological work during the 1935 season were: W. C. Beatty, Jr., Denver, Colo.; C. T. R. Bohannon, Washington, D. C.; A. L. Coffin, Fort Collins, Colo.; L. C. Eiseley, Lincoln, Nebr.; H. L. Mason, Silver Spring, Md.; Carl F. Miller, Tucson, Ariz.; Roger Mixter, Boston, Mass.; Wayne Powars, Greeley, Colo.; and George L. McLellan, Lodi, Calif.

The Lindenmeier site, as described in the preliminary paper issued in the spring of 1935,<sup>2</sup> is located on an old valley bottom, which, owing

<sup>2</sup> Roberts, 1935.



to the eroding away of the ridges which once bordered it along one side, now constitutes a terrace above an intermittent tributary to a series of streams which ultimately join the South Platte River. The work in 1934 was mainly confined to a deep deposit of midden material exposed in the side of a ravine that cuts across the terrace in the zone of former occupation, but traces of the cultural stratum were also noted at several points along the edge of the terrace. The plan of procedure in 1935 called for the digging of two large trenches between the edge of the terrace and the bank of the ravine (pl. 1, fig. 1). The trenches were started several hundred feet apart at places where bones and stone chips had been found the previous autumn but were directed so that they would converge at the pit where most of the specimens were obtained. This method of digging was adopted for the purpose of exposing a complete cross-section of the fill overlying the old valley bottom and of determining, if possible, where the artifacts found in the deep deposit had originated.

The expedition did some work near the location of the original Coffin finds. The preliminary report on investigations at the site discussed its discovery by Judge C. C. Coffin and his son A. L. Coffin, and the subsequent reporting of its existence to the Smithsonian Institution by Maj. Roy G. Coffin, professor of geology at Colorado State College.<sup>3</sup> The paper also pointed out that the material described in it came from a place a quarter of a mile to the west of that where the first Coffin finds were made. In discussing the latter the writer mentioned the fact that most of the Coffin artifacts had been picked up from the surface, which is the top of a hard, compact, tufaceous layer, an Oligocene deposit, which underlies the entire site. The artifacts had undoubtedly been in top-level material that had been eroded away by wind and water. Because of their weight the implements remained until picked up. Portions of the sand, gravel, and nodule layer which had overlain the compact deposit remained in some places, and the Coffins had found a few objects on the contact line between the two. After an inspection of the location the writer was dubious about the possibilities of getting more information than that already obtained by Judge and Major Coffin but had discussed a tentative plan of procedure with A. L. Coffin. When the deeply buried deposit was discovered in the ravine bank, indications were that it was a more likely place for obtaining specimens from undisturbed layers, and activities were concentrated at that point.

During the winter and early spring following the writer's first excavations, the Coffins visited the site a number of times, and in

<sup>3</sup> Roberts, 1935, pp. 1-3.



scratching around the remaining "islands" of top-layer earth A. L. Coffin and Major Coffin uncovered some bones at the original location. On the strength of this evidence, trenches were dug through a portion of the area where erosive action had not completely uncovered the basic stratum. This was a fortunate procedure because, contrary to the impression of the preceding autumn, there was evidence still in situ. A bone pile comprising the remains of several individual bison was located there. Some of the skeletons were partially articulated and, in common with a majority of the separate bones, were in a good state of preservation. Although a number of the bones had been cut and split, the material as a whole was much more satisfactory from the standpoint of the paleontologist than that obtained in the earlier work. It made less debatable the identification of the species of bison present at the site and corroborated the conclusion reached the previous year from very scrappy evidence.

Besides animal bones, a number of invertebrates were obtained at the site. Identification of the mollusks contributes further to the knowledge of general conditions at the time of occupation. Fragments of charcoal were saved in the hope that the wood could be identified and contribute still more evidence on the physiographic environment. This material is being studied by Dr. Ralph W. Chaney, of the University of California, but no report on it has been received. Samples of the soil in which the remains were found were tested for possible fossil pollens in a further effort to broaden the picture. This work was done by Margaret Kaeiser, of the University of Oklahoma, under the direction of Dr. Paul B. Sears, head of the department of botany at that institution. Unfortunately, there was no evidence of pollen in the dirt. Dr. Paul S. Conger, custodian of diatoms, United States National Museum, examined earth samples for fossil diatoms, microscopic unicellular algae that inhabit fresh and salt water, but found none. He noted fragments of sponge spicules, although they were too disintegrated for identification.

In addition to the work done by the Smithsonian Institution's field party, investigations were conducted at the Lindenmeier site by the Colorado Museum of Natural History, Denver. Their excavations extended from June 14 to September 1. Jack Cotter, Harley Goettsche, and Robert J. Lanberg comprised the Denver expedition. J. D. Figgins, at that time director of the Denver Museum and now with the Bernheim Foundation near Louisville, Ky., visited the site a number of times while his men were at work there. Mr. Figgins and Mr. Cotter made available to the present writer, for study, all the material

obtained from their excavations, and Mr. Cotter also furnished a copy of the manuscript that he submitted as a report on the work.

The Denver Museum party dug a series of 15 test pits. These were spaced at intervals extending from the area of the original Coffin finds to some distance beyond the main Smithsonian trenches. The pits gave a good sampling of the character of the deposits across the portion of the site lying between the terrace edge and the ravine bank on a line approximately at right angles to the trenches. One of the test holes west of the large trenches penetrated the artifact-bearing stratum at what appeared to be a likely spot. With this as a starting point an area 30 feet by 30 feet was laid off and completely excavated. This large pit (map 1) yielded most of the specimens obtained by the Denver group.

#### THE MAIN TRENCHES

As previously stated, the major part of the 1935 work consisted in driving two large trenches from the edge of the terrace toward the deep pit where the 1934 activities were centered. The trenches were dug in 10-foot sections. Their bottoms followed the top of the light-colored substratum just below the old soil level which was the surface of the ground at the time when the site was inhabited by the makers of the tools found there. Detailed drawings were made of the faces and side walls in each section, and these give a minute record of events involved in the growth of the valley fill. All of the material obtained from each section was so designated, and in addition the positions of specimens in the section were carefully noted. Only one trench was carried through to completion (pl. 1, fig. 2). The other was stopped when it became apparent that the evidence from it would largely duplicate that from the first. The completed trench was 270 feet (82.296 m) long, 10 feet (3.048 m) wide, and sloped from a depth of 3 feet (.914 m) at the edge of the terrace to 17 feet (5.182 m) in the bank of the ravine. When the work had been completed, the section drawings of the sides of the trenches were combined into one long diagram for each wall (fig. 1). A number of interesting factors are brought out by these diagrams.

The numbers extending across the top of the drawing (fig. 1) indicate the pegs which marked off the courses of the trenches. They were set every 10 feet (3.048 m). References to specific sections in the ensuing discussion will be by number. For example, section 1 consists of that portion lying between pegs 1 and 2, section 2 between 2 and 3, and so on. Neither trench had a complete zero section. As there had already been some digging at the terrace edge, when the presence of

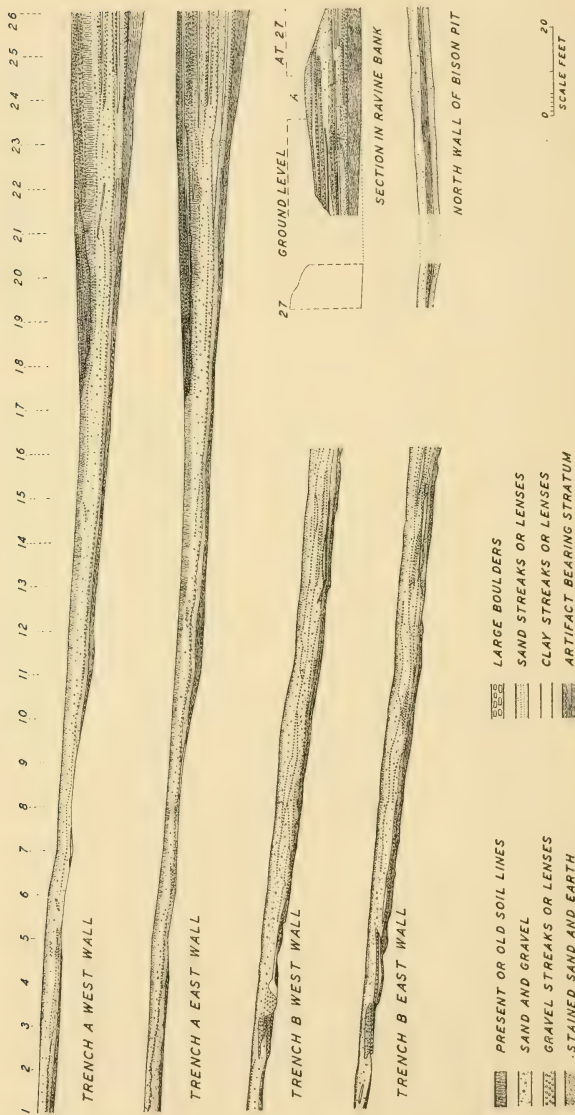


FIG. 1.—Cross-sections of trench walls, face of deep pit in ravine bank, and sides of bison pit.

bones and artifacts was noted the previous year, the initial pegs were set a short distance from the old excavations. Loose dirt was cleared from the pits and the walls were straightened to correspond to the lines of the proposed trenches. The remaining earth was worked out up to the number 1 pegs. This made possible the starting of each trench with a clear-cut number 1 face. Objects found in the zero sections were so recorded, but the careful drawing of section sides and faces was started with peg 1. At the lower end of trench A there is no drawing of the detail of the fill between pegs 26 and 28. This is due to the fact that the material in those sections was worked back on a 48-foot (14.630 m) face from the deep pit in the ravine bank, and the walls of the big pit did not correlate properly with those of the narrower trench in making a composite diagram. There was little change, however, in the last 20 feet (6.096 m). The main difference was in the deepening of the dark earth stratum in which the archeological objects are found.

The method followed in digging was that of stripping off the deposits layer by layer, from top to bottom, in a single section. The upper strata were removed by the use of pick and shovel. Careful check at various places about the site had demonstrated that the higher levels were so nearly sterile, from the standpoint of artifacts, that it was not necessary to subject them to the same careful kind of excavation as that employed in the specimen-bearing stratum. The latter, which rested upon the top of the hard Oligocene clay, was dug with small tools, bent awls, hand trowels, etc., and all the earth sifted through screens (pl. 2, fig. 1). The slow, meticulous method of digging had several advantages. There was little danger of breakage, it made possible a careful check of the provenience of each specimen (pl. 2, fig. 2), and it facilitated following the top of the clay bed. A different method was adopted for the last five sections in trench A. This was necessitated both by the increase in the amount of overburden and by the shortening of the time available for the work. In these sections the upper layers were removed by the use of a team, plow, and scraper. The lower levels, however, were subjected to the same careful hand technique used throughout most of the work. The chief drawback to the use of the plow and scraper was in the fact that it prevented the drawing of diagrams of each section face. Some information was no doubt lost because of this condition, but inasmuch as the side walls were diagramed, most of the essential evidence on changing conditions in the valley filling process was obtained from the sections.

In drawing and recording the deposits in each section, all of the animal burrows were noted. Even though many of them had long

been abandoned and were completely filled with compact material, they were easily seen. Wherever they occurred in the side walls or faces of the sections, they were included in the diagram. They have not been indicated in figure 1 because they are not deemed essential to the discussion of the valley fill. One interesting fact came out of the check on the animal burrows, however. It has been a common practice on the part of many to discount all finds made in comparatively deep deposits by attributing their location to the work of animals. They explain that the specimens were either carried down by such creatures or fell into holes made by them. Out of a total of 983 burrows, only 1 contained an implement. When it is borne in mind that 750 implements were recovered, the extremely small percentage for such an occurrence becomes apparent. Furthermore, indications were that the animal concerned had been attempting to remove the stone from the burrow and that it had been unable to do so. Those who have excavated in the Southwest, where sites riddled by prairie dogs are a common feature, have frequently noted that the animals will bring objects to the surface but that it is extremely rare to find specimens carried down into the lower reaches of the burrows. The figures from the Lindenmeier site certainly show that the "animal burrow argument" against the authenticity of finds in low levels has been considerably overemphasized.

Trench A, the completed one, did not exhibit as many complicated features in its upper or shallower sections as did trench B. Nevertheless, there were several worthy of comment. The dark, artifact-bearing stratum disappeared toward the end of section 4 and did not appear again until the work had penetrated into section 9. The soil covering over the tufaceous base had been removed by some agency, presumably wind, prior to the deposition of the upper layers. Despite evidences of a small stream channel cutting across sections 6 and 7, the erosion does not seem to be attributable to water action. The top of the clay bed gave more the appearance of a wind-scoured surface. As a matter of fact the bottom of the trench followed across the summit of a ridge in sections 5 to 9. This ridge had run at an angle to the line of the present valley and is quite apparent in the bank of the ravine down stream from the pit where trench A cut into the gully. Test holes were sunk in the floor of the trench in these sections to make certain that the black stratum did not go below the clay and that the latter was actually the top of a ridge and not a lens laid down subsequent to the deposition of the specimen-bearing layer. The few artifacts and stone chips found in this part of the trench were lying directly on top of the basic stratum. As a further check on the situation



a smaller trench was dug through the area east of sections 3 to 5. This work revealed that the artifact-bearing layer there was on a slope dropping away from the ridge.

The black layer appeared again in section 9 and continued unbroken, though varying in thickness from section to section, through to the ravine. At first it was thought that the greater depth of the cultural layer in sections 10 to 13 was due to the washing down of material from the area above. Evidence of water action was not apparent, however. There undoubtedly was some drift from the higher ground but not in sizeable quantities, and the increase in thickness may possibly be explained by the fact that the black stratum overlay a slight declivity in the top of the old clay bed in sections 11 and 12.

The lower sections in trench A demonstrate clearly the factors involved in the filling of the old valley and the raising of the surface level from that occupied by the makers of the implements to the present top of the ground. There are numerous layers of water-deposited material and evidences of the shifting of intermittent stream beds. Various soil lines indicate intervals when conditions were static and vegetation flourished unhampered by material carried down from the higher slopes. In the upper levels of sections 17 to 22 an old stream bed is clearly shown. It was cut, the water course shifted, and the channel filled before the present ravine became a feature of the terrain. Despite the fact that conditions in the West are such that cutting and filling may take place at a rapid rate, considerable time is probably represented by the accumulation in the valley bottom.

A few interesting things may be noted regarding the occurrence of specimens. The most prolific sections in the yield of implements were 12 to 16, the greatest number coming from 16. The largest amount of chipper's debris centered in 13, 14, and 15. In section 15 one series of flakes totalling 111 was found in a 4-inch (10.16 cm) radius, with 78 of the chips in a single pile. Nearby were some hammerstones, and several broken implements occurred in the material from the section. All the fragments from these implements were obtained, and it was possible to restore them. In the lot was a Folsom point represented by two pieces found 4 feet (1.219 m) apart. Section 14 yielded the only definitely worked piece of bone, a thin disk with a series of lines cut around the edge. The percentage of implements by sections is as follows: 1, 3.6 percent; 2, 5.3; 3, 2.5; 4, 1.1; 5, 1.1; 6, 0; 7, 0.4; 8, 0.4; 9, 1.8; 10, 3.6; 11, 3.6; 12, 7.8; 13, 10.6; 14, 7.5; 15, 8.5; 16, 14.5; 17, 3.6; 18, 3.1; 19, 3.6; 20, 0.4; 21, 1.1; 22, 0.4; 23, 2.1; 24, 2.1; 25, 6.7; 26, 4.6. The material from the deep pit in the ravine bank is not included in these figures because the work done there was



not on a comparable basis. However, the yield per square foot in trench A was greater. The proportions average 1 specimen to 0.9 square foot for trench A, and 1 specimen to 6.5 square feet for the pit.

Cut and split animal bones occurred in sections 1, 10, 11, 12, and 16. Those in 10, 11, and 12 did not constitute a continuous deposit through the three sections. In 10 the bones extended across the trench from the middle of the section to within a few inches of the face of number 11. In the latter they were along the west wall in the half towards the face of 12. Those present in the bottom of 12 started 1 foot (30.48 cm) beyond the face of the section and continued for 6 feet (1.828 m) along the east wall. The lens extended into the trench 2 feet (60.96 cm) from the east wall. The bones from the first sections were very fragmentary and in a poor state of preservation. Those in 10 were in better condition and indicated that they came from several young bison. The implements and chips of stone in the section were intermingled with the bones. In section 11 were numerous small fragments, most of which show the effects of burning or at least are partially charred, and a number of bison foot bones which had been split. Several large stones, hammers and choppers, accompanied the bones. The material in 12 consisted of exceedingly scrappy fragments, presumably bison but too shattered for identification. Section 16 contained a few scattered pieces which appear to be from the leg bones of a bison.

The bottom of trench B had a more gradual slope than did the bottom of A, owing to the fact that the ridge which crossed A in its sections 5 to 9 was not present in B. Trench B ranged in depth from 3 feet (.914 m) at the upper end to 7 feet 6½ inches (2.298 m) at the face of section 16, where work was stopped. Sections 1 to 7 (fig. 1), trench B, gave distinct evidences of the channel of a small stream that formerly meandered down the slopes across that portion of the terrain. The flow was probably intermittent, water being present only after heavy rains or when the snows of winter were melting, and consisted of the run-off from the higher ground above the site. The runlet had changed its course and size several times. Originally it had swung in a slight curve from west to east through section 2 to section 1. Owing to subsequent filling and widening, it moved down the slope to section 3, where its course turned to such an extent that it followed the direction of the trench through sections 4, 5, and 6. In section 7 it swung off toward the west again and passed beyond the bounds of the trench. Considerable quantities of clay were deposited in the channel, and after it had become appreciably shallower the water again began to cut, although it formed a much smaller bed along the

course of the older one. These features do not show as well in the diagrams of the trench walls as they do in the drawings of the section faces, which are not reproduced in this report, but study of sections 2 and 3, figure 1, will show their beginnings as they appeared in the walls. The significance of this old stream is that its original channel was cut after the deposition of the soil layer which contains man-made objects and that it removed this dark stratum as it progressed. Furthermore, the channel and its history as briefly sketched provide evidence that there was a higher and more extensive ridge above the site than that of the present day. Now there is not sufficient run-off, even after the heaviest rains, to form such a course. Numerous sand and gravel lenses scattered along the length of the trench demonstrated the occurrence of subsequent washes which carried material down from the higher slopes. With the exception of sections 13-15 there were no clear-cut channels, however. Those sections showed that a wide, shallow stream had crossed that point after considerable material had been deposited above the old occupation level.

In trench B the largest showing of specimens was in sections 7 through 10, although 1 through 5 had a consistent yield. The percentage dropped in 6 and then swung upward to the peak which was reached in 9. It then dropped off to section 12 which contained no implements, although some chips and flakes were found there. From this point to the end of the trench there was a gradual increase in returns, but the yield was not as good as in the earlier sections. In section 5 the black layer on either side of the channel contained a number of large nodules and flakes. None were found in the channel, however. On the west side of the trench at the lower end of section 12, just below peg 13, was a shallow, saucer-shaped depression in the top of the old clay bed. The concavity held a quantity of charcoal and suggested that it might have been a shallow fire pit, although the underlying clay showed no signs of the effects of heat. It is possible that a small fire burning for a short time in such a pit would not cause sufficient discoloration to remain over a long period of years or that such reddening as did take place was subsequently leached out. There were some small fragments of burned bones in the charcoal and around the borders of the basin. The lens of charcoal extended into section 12 a distance of 2 feet 6 inches (76.20 cm). It did not appear in section 13. It projected into the trench for 2 feet (60.96 cm) in section 12. The percentages of implements for the various sections in trench B are as follows: 0, 1.7 percent; 1, 7.9; 2, 6.2; 3, 5.2; 4, 7.1; 5, 6.2; 6, 1.7; 7, 7.9; 8, 15.8; 9, 17.5; 10, 9.7; 11, 4.4; 12, 0; 13, 0.9; 14, 2.6; 15, 5.2.

Bone fragments were not as plentiful in trench B as in trench A; also, the pieces found were as a rule smaller and more fragmentary. Material of this type came from sections 1, 7, 8, 9, 12, 14, and 15. Sections 7 and 12 contained numerous burned and partially charred pieces. An interesting correlation is suggested by the occurrence of the many burned fragments in trench A, section 11, and trench B, section 12. These two sections were located along the same contour line, and their bottoms, the old occupation level, had only a slight slope so that the original surface would have provided a comparatively flat area, a place suitable for camping purposes. The presence of charcoal in the concavity in the old surface in section B-12, the burned bones in both B-12 and A-11 together with the large stones and choppers in the latter—as noted in the discussion of trench A—constitute good evidence that the makers of the Folsom points had actually tarried for a time along that portion of the slope. If the trenches did not cross a portion of the real campsite, they at least bordered upon it. This is further substantiated by the fact that subsequent sections in A were those from which the most specimens came.

In discussing the big pit in the ravine bank in the preliminary report, mention was made of evidence indicating that small ponds or marshy places had been scattered over the old valley bottom.<sup>4</sup> It was suggested that the deep level seemingly constituted the peripheral vestiges of one such spot, the main portion of which was washed away when the present ravine, possibly an older one also, was formed. Information gleaned from the lower sections of trench A corroborates that conclusion as well as the suggestion that the archeological objects obtained there represent midden material that was deposited along the edges of a shallow pond or slough. Some of the specimens no doubt drifted down from the higher levels and others may have been tossed out to sink through the mire to the top of the clay stratum where they are found today. They were not dropped on an occupation level, as were those from sections 12-16, because from section 23 through to the ravine the black stratum gave every indication of an underwater deposit of the kind generally associated with bogs.

The valley fill, as revealed in cross-section by the trenches, shows that the old level of occupation consisted of a soil layer, several inches in thickness, resting on a tufaceous substratum, a Tertiary deposit dating from the Oligocene. The soil layer probably was produced by the natural decay and break-up of the top of the Oligocene bed and subsequent growth of vegetation over the area. There was no evidence

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<sup>4</sup> Roberts, 1935, pp. 11, 14.

of deposition by water. No information was obtained to indicate what agency was responsible for the original scouring of the valley and removal of material down to the Oligocene stratum or when such action took place. After the abandonment of the location by its human inhabitants, material from the higher levels was washed down across the site. The first layer to be deposited consisted of stained sand and earth, presumably occupation level material from the upper slopes. This in turn was covered by sand, gravel, and boulders swept down into the valley from its bordering hills. Then the alternating periods of erosion and building up set in as demonstrated in the lower sections of the trenches. As previously stated, all of this change could not have been extremely rapid here because ridges which contributed to some of the valley fill have since completely disappeared, being weathered away in the opposite direction. Furthermore, there are good indications that the central portion of the valley, which lies to the north of the ravine and the archeological site (map 1), now consists of secondary fill. The material which raised the old bottom to the level represented by that above the deep pit was subsequently washed away and the area again built up with sand, gravel, and rocks carried down from the ridges to the west and north of the site. That the original fill, represented by the deposit above the deep pit and the artifact bearing stratum in the area crossed by the trenches, was not disturbed may be attributed to the fact that it was far enough up the opposite slope to escape forces at work on the floor of the valley. This feature is one, however, which belongs more properly in Dr. Bryan's discussion of the geology of the site and will not be considered further at this point. The geologic report will appear in a later publication on the work at the site.

#### THE BISON PIT

The excavation where the bison bones were uncovered measured 20 feet (6.096 m) by 47 feet (14.326 m) (map 1). Owing to erosion by wind and water, as mentioned in an earlier paragraph, the deposit was not as deep as in the area where the trenches were dug. The bones ranged in depth from  $10\frac{1}{2}$  inches (26.67 cm) at the upper side of the pit to 3 feet (.914 m) below the surface along the lower side. The position of the strata here differed slightly from that observed in the main trenches. The object-bearing layer did not consistently follow the clay substratum. It rested upon a bed of stained sand and earth which in turn lay directly on the clay. A wholly satisfactory explanation for this condition was not obtained from the digging. The best suggestion which can be offered at this time is that the particular

animals were killed before a definite dark soil layer had been built up. Some of the bones extended down into the stained stratum. Exposure of a larger section in this area is probably essential to an understanding of the various factors responsible for the situation. The deposit above the bones was similar to that in the upper layers of the trenches, namely, sand, gravel, and some boulders, with a thin soil line at the present surface.

At least nine individual bison are represented in the collection from this location. Many of the bones, including several legs, were still articulated when uncovered (pl. 3, fig. 1). The remains of one creature were found with a forequarter, most of the ribs from one side, and the vertebral column still intact. The skull, in a somewhat damaged condition, was nearby. Portions of other skulls were obtained, but they are all too fragmentary to be of material assistance in the identification of the species. The most striking find consisted of a vertebra with the tip end of a projectile point in place in the foramen for the spinal cord (pl. 3, fig. 2). This bone was in position in the center of a group of articulated vertebrae, and when it was removed from the ground and was being cleaned by L. C. Eiseley, graduate student from the University of Pennsylvania, the point was discovered. Hafted on either an arrow or spear shaft, it had apparently been driven into the animal and then broken off at the end of the longitudinal groove. The wound may not have been directly responsible for the creature's death, but it would have crippled it to such an extent that a killing blow could easily have been administered. This was not the only implement from the pit, however, as 33 additional specimens of the stone chipper's work were found in association with the bones. These objects consist of points, portions of points, various types of scrapers, blades, flakeknives, and graters. Two flakes with chipped cutting edges accompanied the bison skull, and several fragmentary points were lying between components of articulated segments in such a way as to suggest that they had been in the flesh of the animals.

The assemblage in the bison pit recalled in some aspects features observed at the quarry where the original Folsom finds were made.<sup>5</sup> Evidence at the latter place indicated the culmination of a hunt and the killing of animals around a water hole or marshy spot. After as much of the flesh as could be carried away had been removed from the carcasses, they were left to sink in the mire. Through the course of time natural agencies drained the swampy ground and covered the site with earth washed down from higher levels in the vicinity. No

<sup>5</sup> Cook, 1927; Figgins, 1927.



traces of an occupation level or camp were found at Folsom—only the signs of the kill. In this respect it was like the bison pit. Since most of the material scattered over the Lindenmeier site is so scrappy in its nature, the discovery of partially articulated skeletons and numerous whole bones was fortunate. Just why the dismemberment of these animals had not been carried to completion can only be postulated. They may have been killed shortly before the group moved from the site and only such portions taken as could be disposed of immediately. The camp possibly was oversupplied with meat and as a consequence only the hides and choice cuts were removed. Then again, they may represent a winter kill when pelts were the chief objective, the winter coat being superior for robes or blankets.<sup>6</sup>

There is no evidence to show the manner of hunting or methods of butchering. It must be borne in mind, however, that the period here represented long antedates the era of the horse in North American Indian cultures and that the chase had to be conducted on foot, the practice in vogue among later peoples when encountered by the first Spanish explorers in the Southwest.<sup>7</sup> This custom probably called for greater cunning and skill, if not actual bravery, than did the method of hunting after the horse became a prominent accessory in the Plains cultural pattern. It was necessary for the hunter to get close enough to the bison to use his stone-tipped weapons with success. By analogy, on the basis of later customs, it may be suggested that Folsom man erected brush-shelters or blinds close to the ponds and watering places frequented by the bison and bagged the creatures from ambush. Vicente de Saldivar Mendoca observed such a practice when he visited the buffalo plains in 1598 as sargento mayor of the Oñate expedition.<sup>8</sup> It is also possible that the hunters camouflaged themselves in a manner similar to that reported at a much later date by Catlin. He described the way in which Indians covered themselves with wolf skins and crawled on hands and knees to within a short distance of the desired game and then killed it.<sup>9</sup> Wolves were numerous and commonly followed the herds of buffalo, the latter paying little attention to their presence.<sup>10</sup> Bones from the wolf were found here, so that hunting in that fashion was not beyond the range of possibility.

Butchering an animal the size of those represented by the material from the bison pit would not be an easy task. It seems obvious that

<sup>6</sup> Catlin, 1841, vol. I, pp. 253-254.

<sup>7</sup> Espinosa, 1933, p. 137.

<sup>8</sup> Bolton, 1916, p. 230.

<sup>9</sup> Catlin, 1841, vol. I, p. 254.

<sup>10</sup> Winship, 1896, p. 528.



the skinning and cutting up of the meat must have been done where the slaughter took place, in this instance at no great distance from the camp. The situation at the time of occupancy would have been favorable to the brush-blind type of hunting. A slough or marshy spot had existed in the old valley floor not far from the point where the bones were found—this was demonstrated in one of the Denver Museum test pits. A screen placed on the slope above would have made an ideal place to await the coming of the bison. The nature of the soil layer indicated that there was fairly heavy vegetation around the water hole, probably coarse grass and reeds, which would protect the meat from dirt and sand during the process of skinning and cutting up an animal killed at this place. The handling of the carcass no doubt presented a problem of some difficulty, as there were no mechanical means for transporting it or to facilitate turning and lifting. Such work had to be done by manpower alone. The only tools available for the dismembering operation were those of stone or perhaps bone.

The nearest approximation to the description of such an undertaking is probably that by Castañeda. The latter was the chronicler for the Coronado expedition, which penetrated into the buffalo area in 1540. Members of that party had an opportunity to observe the Indians under conditions comparable to those of earlier centuries. In his account of the skinning of the bison Castañeda said: "They cut the hide open at the back and pull it off at the joints, using a flint as large as a finger, tied in a little stick, with as much ease as if working with a good iron tool."<sup>11</sup>

Other documents, one attributed to a friar accompanying the Coronado party,<sup>12</sup> one by Luxán,<sup>13</sup> and Fray Juan Augustin Morfi's *History of Texas*,<sup>14</sup> give good accounts of the use to which various parts of the animal were put. The skins were employed in the making of tents, clothes, footgear, and rope. The sinews were used to make thread for sewing their clothes and tents, and for wrapping shafts. The stomachs served as pitchers and vessels, the intestines as containers of fat and of marrow. Awls were made from the bones. The horns were cut into spoons, cups, and ornaments. The hoofs were converted into glue to aid in fastening projectile points in shafts. The brains were used in tanning and softening the hides. In view of all this, it is little wonder that the bulk of the bone material from the site consists of scraps and splinters. Even in the bison pit, which

<sup>11</sup> Winship, 1896, p. 528.

<sup>12</sup> Winship, 1896, p. 570.

<sup>13</sup> Hammond and Rey, 1929, pp. 120-121.

<sup>14</sup> Castañeda, 1935, p. 67.

contrasted sharply with other portions of the site, many of the bones were cut and split, and several of the skulls had been battered and chopped into small pieces.

The bones from the bison pit were submitted to Dr. C. L. Gazin, assistant curator of paleontology, United States National Museum, who kindly furnished the following notes:

The Fort Collins material represents an extinct species of bison and should probably be referred to *Bison taylori*. The horns of the skull are very incomplete, but from the size of the proximal portions of the horns, the breadth of the cranium, and the length of the rostrum it is clearly not a living type.

Comparisons are handicapped by lack of comparable fossil material in our collections outside of Alaska and Minnesota. It has been necessary to rely largely on published illustrations and descriptions of the numerous bison which have been designated as distinct species. It is obvious that too many names have been applied to North American bison and some of the older types are hardly adequate for clear diagnosis. Several of the known species are eliminated in comparisons, however. The Fort Collins material apparently could be referred with equal readiness to *Bison occidentalis*, *Bison taylori*, or *Bison oliverhayi*, among those which remain, and there seems to be some doubt as to the validity of one or more of these.<sup>15</sup>

The skull resembles, and approximates in size, a skull from Kansas identified by Lucas as *Bison occidentalis*, which was the first reference to this Alaskan species of material from the United States proper. This determination by Lucas probably furnished the basis for continued recognition of the species in the middle western region. The Fort Collins skull is intermediate between the types of *Bison taylori* and *Bison oliverhayi* from Folsom, N. Mex., in breadth of the cranium at the postorbital constriction, but the entire length of the skull is as great as, or perhaps somewhat greater than, that of *Bison taylori*. Unfortunately, the incompleteness of the horns obviates detailed comparisons of these structures; however, the greatest diameter of the basal portion of either horn about equals that in *Bison taylori*. Characters of the teeth which have been used to distinguish species of bison are of doubtful value and do not help in the present case.

The proportions of most of the limb elements are slightly less than the measurements given by Hay and Cook for *Bison taylori*, although a few of the foot bones are larger in their respective measurements. The various limb bones and vertebrae, other than indicating an animal of distinctly large size, are of little or no diagnostic value in determining the species.<sup>16</sup>

#### ARTIFACTS

The specimens collected from the excavations consist of points, scrapers, graters, chisel-graters, choppers, large blades, flakeknives,

<sup>15</sup> The scrap bones secured in the autumn of 1934 were identified by J. D. Figgins as being from both *Bison taylori* and *Bison oliverhayi*. See Roberts, 1935, p. 31.

<sup>16</sup> For a discussion of *Bison taylori* and *Bison oliverhayi* see Hay and Cook, 1930, Figgins, 1933.

hammerstones and rubbing stones, and worked bones. Pieces of hematite show the effects of having been rubbed for pigment. There are numerous flakes, too nondescript in character to be called implements, which exhibit signs of workmanship. The collection also contains a large number of channel flakes, the long spalls removed in the fluting of the projectile points. Varieties of stone represented in the implements are jasper, chert, chalcedony, moss-agate, quartzite, petrified wood, geyserite, limonite, granite, quartz, and sandstone. Most of the chipped tools, the cutting and penetrating implements, were made from the chalcedony, chert, jasper, moss-agate group, the "flint" of the amateur collectors. This type of material is well adapted for use in tools and wherever available constituted the preferred stone of the implement fashioners. The harder quartzite and petrified wood were employed but, in addition to being more difficult to work, did not produce as good finished products. On the other hand, they were better for hammers and mauls, and numerous examples show that they, as well as the quartz and granite boulders, were used for that purpose. Sandstone is suitable only for rubbing, polishing, and sharpening bone tools and was so employed at this site.

The percentages of specimens found at the various places where excavations were made is as follows: Trench A, 37.6 percent; trench B, 15.2; the big pit in the ravine bank, 17.5; the bison pit, 4.4; the small trench east of sections 3-5, trench A, 10.7; miscellaneous, scattered surface finds and specimens scratched out in prospecting along terrace edge and ravine bank, 14.5.

#### POINTS

There is an interesting range in the size and variety of points (pl. 4). This group constitutes 11.3 percent of the specimens in the collection. The predominant type of point is the characteristically fluted Folsom in its two forms, the long and slender one with tapering tip, and the short, broad style with the maximum breadth of blade occurring close to the tip end.<sup>17</sup> Although most of the specimens are fragmentary examples, there is sufficient material to show that the two forms were about equal in number. The short, stubby examples, designated form A in the preliminary paper, range in size from one with a length of 22.5 mm, breadth of 14 mm, and thickness of 3.5 mm, to one with a length of 70 mm, breadth of 35 mm, and thickness of 6 mm. The long, slender specimens, the B form, have a range between one with a length of 23.5 mm, breadth of 13 mm, and thickness

<sup>17</sup> Roberts, 1935, pp. 15-16, fig. 2.

of 2 mm, and one with a length of 60 mm, breadth of 23 mm and thickness of 4 mm.

The preponderance of broken specimens found at most sites has been pointed out by numerous writers. In the 1935 series from the Lindenmeier site the situation remains unchanged, as 87 percent of the points are only fragmentary examples. In general this condition may be attributed to the brittleness caused by the fluting. The removal of the longitudinal flakes from each face so thinned the points that they became extremely fragile. At the present site, however, two other factors must be considered, namely, that many points were broken in the making, and that the collection contains specimens which were never completed. The purpose of the grooves is not known, although a number of explanations have been made to account for them. It has been suggested that the fluting was to facilitate hafting, the split end of the shaft fitting more snugly into the grooves than it would if the point had a convex basal surface. Other interpretations are that it was to improve the penetrating qualities, to permit the head to break off in the animal, to allow the head to slip out of the foreshaft, to promote bleeding, and to reduce the weight. No doubt a number of such ideas influenced the development of this typical feature. The most important, however, in the opinion of the present writer pertain to the quality of penetration and the hafting.

The method of shaping and chipping Folsom points was discussed at some length in the previous report and need not be described in detail in this paper.<sup>13</sup> It will suffice to say that the evidence from the recent work substantiates that of the preceding season and corroborates conclusions drawn from it. These conclusions were that the points were first shaped, then the channel flake was removed by indirect percussion applied to a nubbin or small "seat" left in the center of the concavity when the base was chipped. Finally, the edges were retouched. The 1935 material adds one significant factor, however, which was suggested by the earlier specimens, but the evidence was not conclusive enough to warrant its mention in the preliminary report. This factor is that the tip was left in a roughly rounded state, not pointed, until after the channel flake was removed. Its shaping constituted a part of the secondary chipping by which the edges were refined. Several specimens in the new series definitely show this to have been the practice. Two examples, both broken into several pieces in the process of manufacture and tossed aside uncompleted, clearly demonstrate the feature.

<sup>13</sup> Roberts, 1935, pp. 18-21.

The broken material from the 1935 work contains more tip ends than that of 1934, although the butt ends still comprise a large percentage of the series. Most of the tip ends came from the bison pit, and the inference is that they had been embedded in the flesh of the animals whose bones were found there. In discussing the prevalence of butt ends in the previous finds it was suggested that the circumstance could be attributed to the replacing of damaged points. Many must have snapped off in the killing of game. This is illustrated by the tips in the bison pit and by the one in the vertebra. Undamaged shafts were no doubt retrieved and carried back to camp to be fitted with new points. The fragment of the old one remaining in the shaft would be the butt end, and in the remounting process it would be tossed aside to remain in the debris of accumulation. Such an explanation, of course, refers only to fragments which show that they formed part of a completed point; it would not apply to butts from those broken in the making. The basal portions were not always discarded, however, as examples in the collection show that it was not an uncommon practice to take a butt which had lost its tip and rechip it so that it again had a point capable of penetration. Specimens in this group are extremely stubby and flat-pointed.

There are a number of points in the collection which are not of the characteristic Folsom form. One type in the variant group consists of small points made from fortuitous flakes, often from portions of channel flakes. None of these has the fluting; as a matter of fact, they are too thin to permit the removal of a side spall. They definitely belong in the implement complex, however, and their outlines closely follow the general Folsom pattern. The other type of point is represented by fragments only, but the pieces are so distinct in their nature that they must be considered as representative of a form found in the West which is frequently linked with the Folsom. This is the so-called Yuma. The fragments are from the true Yuma, not from any of the multitudinous subtype varieties. The typical Yuma point, in the conception of the writer, is one which is long and slender. The edges extend approximately parallel from the base—in some cases there is an almost imperceptible narrowing toward the butt—for about two-thirds of the length and then taper to a sharp point (fig. 2). It is oval in cross-section (fig. 2, *b*). The base may be straight across, slightly concave, or deeply concave. Sporadic examples have a small shoulder on one or both sides near the base, thus forming a slight tang (fig. 2, *f*). In the shaping process the main flakes were removed so that the facets extend completely across the face of the blade, usually at a slight angle directed toward the tip. The edges were then



refined by a retouch in which minute flakes were removed, a process comparable to the secondary chipping in the Folsom group.

A large variety of blades and points have been grouped under the name Yuma, and at the present time there is considerable confusion as to what constitutes such a point. In fact it seems that the tendency is to call anything Yuma that is not a true Folsom or a barbed and tanged arrowhead of the recent Plains type. Dr. E. B. Renaud, of the University of Denver, was the first to describe the form and gave it the name Yuma. His discussion and classification, including his several subtypes, may be found in his various publications.<sup>19</sup> Dr. E. B. Howard considers the Folsom-Yuma problem at some length in his "Evidence of Early Man in North America,"<sup>20</sup> and J. D. Figgins has written a number of articles on the subject.<sup>21</sup> As the situation

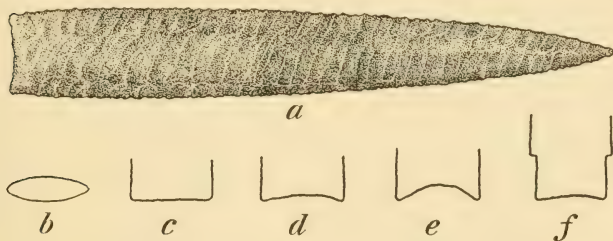


FIG. 2.—Yuma point, *a*; Cross-section, *b*; and base types, *c-f*. (Actual size.)

stands today, it seems essential to reach an agreement on what is meant by Yuma and that its use be restricted to something more specific than its present catch-all connotation.

The importance of the fragments from Yuma type points found at the Lindenmeier site lies in the evidence bearing on their position in the sequence. One came from the latest old stream channel in section B-3. Its position distinctly indicated a later deposition than the black stratum containing the Folsom points. The other specimen came from the black layer. This was in A-23, where indications were that the layer was the bottom of a swamp or bog deposit. The exact position of this example was not obtained, as the point was found in the screen and not in situ. Indications were that it had been in the black fairly high above the contact. Since this cannot be established with certainty, it will be considered as being on a level with the Folsom

<sup>19</sup> Renaud, 1931, 1932, 1934.

<sup>20</sup> Howard, 1935.

<sup>21</sup> Figgins, 1934, 1935.



material. Portions from two other points, not typically the true Yuma type as described in this paper but of a form usually called Yuma, were also obtained. One was above the black layer in section B-8. The other was above the black in the area just east of A-4. The situation may then be summarized as follows: Out of four specimens attributed to the Yuma group, one was in a position that may be regarded as evidence for contemporaneity with the Folsom, and three were later.

The Denver Museum party obtained, in its large pit, four specimens which in a broad sense of the word might be called Yuma. Two of these were from the contact line between the black and the basic substratum. The others were from a higher level in the black. The situation in the deposit where these were found was similar to that in trench A from section 23 through to the deep pit. As a consequence there is the possibility of somewhat later material sinking to a lower level. The only conclusion which can be drawn from the evidence as it now stands is that there was at best only a late contemporaneity between Yuma and Folsom at the Lindenmeier site with a later survival of the Yuma. Subsequent work may throw more light on the subject and change the picture, but at present the Yuma must be considered comparatively late in this immediate district. Furthermore, they are only a minor factor, as only .05 percent of the points from the site can be classified as Yuma, and some of these are of such a nature that their inclusion is highly debatable.

#### SCRAPERS

Implements of this type comprise 32.8 percent of the collection from the 1935 excavations (pls. 5, 6, 7, 8). The tools fall into several major groups. These are the side scrapers, "snub-nosed" scrapers, end scrapers, "thumbnail" scrapers, and scraper edges. The latter consist of pieces from broken implements too indefinite in character to warrant inclusion in one of the other classes. The term "thumbnail" is occasionally used as a synonym for "snub-nosed." In this discussion they are regarded as different types.

The side scraper series represents 56 percent of the group. There is considerable variation in the type of flakes used in their manufacture, their degree of finish, and in their general quality. Some of the implements are light in weight and almost as thin as a sheet of heavy paper. Others are thick and cumbersome. Certain examples are little more than rough flakes with a worked edge along one side only; in some cases merely a portion of the edge shows chipping. Tools in this

group frequently retain part of the siliceous crust of the nodule from which the flake was struck. In contrast are those which display careful workmanship not only of the edges but of the faces as well. The scraping edges, regardless of the quality of the tools, are straight, convex, or concave. Good examples of the concave form are illustrated in figure 3. Several of the implements combine both straight and convex, concave and convex, or all three types of edges. It is possible to separate the side scrapers into a large number of subforms, but for the purposes of this paper the general grouping just described is sufficient.

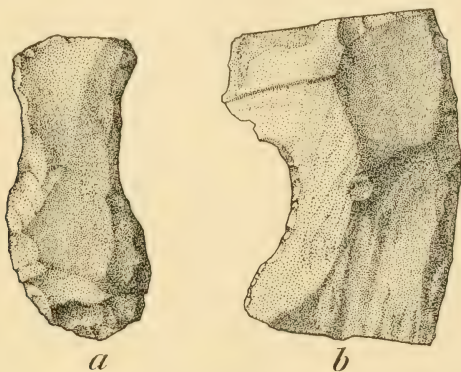


FIG. 3.—Side scrapers with concave cutting edges. (Actual size.)

The “snub-nosed” scrapers are an interesting series and are perhaps the most consistent in type of all the tools in this general category (pl. 8). They comprise 26.6 percent of the scrapers. Despite the fact that there are a number of subforms, the implements, whether large or small, made from good stone or poor, show no marked deviations from the main pattern. All are characterized by one thick, rounded, convex, carefully chipped end. The treatment of the other end, the edges, and the lateral faces varies. Some are untouched, on others the sides were chipped, others show the use of the flaking tool on the lateral faces. Rarely was the bottom of the tool, the ventral surface or side which came off the core, altered in any way. The size range in this group is rather pronounced. They vary in length from 21 to 50 mm, in breadth at the cutting edge from 18.5 to 40 mm, and in thickness from 4.5 to 12 mm.

The end scrapers are more variable and nondescript in form than the types just described. They constitute only 2.4 percent of the series, which might be taken as an indication that they were not as widely used as the other forms. Such was not necessarily the case, however, as numerous implements included in the side scraper class because their predominant features pertain to that form also have an end scraper. So far as shape is concerned, this tool adheres to no particular pattern. Any random flake seems to have sufficed for such an implement. Its main feature is a scraping edge at one or both ends of the flake. The sides and lateral surfaces generally remain untouched. The ends differ from those of the "snub-nosed" group in that they are not thick and bulky, but are more chisellike in form. They are either straight across, slightly convex, or have a sweeping curve not unlike present-day blunt-end table knives. The size range varies between an example with a length of 35 mm, a breadth of 18 mm, and a thickness of 5 mm, and one with a length of 48 mm, a breadth of 23 mm, and a thickness of 4 mm.

The "thumbnail" scrapers are not numerous in the collection. Only 1.6 percent of the scrapers are listed under this classification. They constitute a definite type, however. The name is derived from the close resemblance between their shape and that of the ordinary thumbnail. They are thin, roughly rectangular in outline with a convex scraping edge. Fragments from channel flakes seem to have been favored as material from which to make these implements. The size range is not great. Examples in the collection are from 14 to 15 mm in width, 15 to 17 mm in length, and 2 to 3 mm in thickness.

The broken series or scraper edges comprise 13.4 percent of the scraper group. Most of the specimens are probably portions of side scrapers, but as previously mentioned they are not sufficiently clearcut in form to warrant more definite classification.

A curious implement, the only one of its kind thus far found at the site, is one which can be termed a core scraper (fig. 4). It was made from a small core, not from a flake as were the majority of the tools. The long, slender facets where chips were removed in the shaping process show that the maker was possessed of great skill. Whether the object was the product of a bit of experimental work or belongs to a definite, although minor, type is a question which can be answered only by additional digging. If no other examples are found in a comparable series of specimens, it unquestionably should be considered unique. Core scrapers have been found in parts of Alaska and in some sections of Siberia. This implement is not correlative to the types from those places, however, and it may be that in the last

analysis it should be regarded as an aberrant form of end scraper or "snub-nosed" scraper.

One type of scraper—the turtleback<sup>22</sup>—found during the 1934 excavations is not represented in the collection obtained in 1935. The failure to obtain additional examples indicates that it must have been a very minor form.

No suggestions as to possible uses for the various types of scrapers have been made in foregoing paragraphs. There is no definite knowledge on the subject, but to judge from the later Indians, such tools must have been absolutely essential in the domestic life of their makers. That they constituted an important part of the implement group is shown by the fact that almost a third of the specimens belong in this category. They no doubt functioned in the dressing of skins, the removing of flesh from bones, for cutting bones, and for the

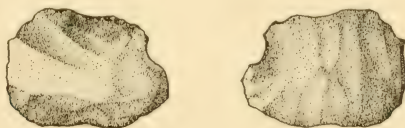


FIG. 4.—Nodule scraper. (Actual size.)

smoothing of spear and arrow shafts. The "snub-nosed" scrapers would be particularly well adapted to the scraping of marrow from split long bones. The convex scrapers, such as figure 3, *b*, are just the type of tool needed in the shaping of wooden shafts.

#### GRAVERS AND CHISEL-GRAVERS

The tools in these two groups are similar in many respects (pl. 9). Although they are definitely related and the terms used to designate them overlap to some extent, there is a distinction between the specimens in these groups. The gravers constitute 5.6 percent of the collection. They are of particular interest because they suggest that the makers of the Folsom points were also adept at some form of the engraver's art. As yet there is only meager evidence of the character of this type of delineation, but the 1935 investigations established the fact that markings were made on bone and soft stone. Fragments from two objects of polished bone, burned in a fire, exhibit finely cut lines which appear to have been components of some kind of decoration. A bone disk with a series of short grooves bordering the edges

<sup>22</sup> Roberts, 1935, p. 24.

on both faces (pl. 9, *c*), suggests the use of an implement such as one of the so-called gravers. A fragment from a similarly marked bone was found by the Denver party, and a portion of a correspondingly shaped and cut object made from soapstone—found by Maj. R. G. Coffin—shows that materials other than bone were subjected to ornamentation of a type which could be executed only by use of such a tool.

Another possible function for the graver type of point has occurred to the writer, namely, its use in tattooing. This custom prevailed to a greater or less extent throughout the country among the later Indians and may have been one of the traits of Folsom man. The small, very sharp tips would readily puncture the skin for the application of pigment. Unfortunately, the “canvas” on which such designs are drawn is highly perishable, and there is little likelihood of finding direct evidence that tattooing was done.

Most of the gravers consist of chance flakes modified only by the presence of short, needlelike points on one side or end. Any piece of stone, provided it was thin enough, was suitable. Sometimes a channel flake (pl. 9, *a*), was employed, and occasionally a fragment from a broken scraper. On the whole, however, nondescript scraps from chipper's debris were all that the maker required. The small sharp points were not fortuitous: they were definitely chipped. They differ from the usual drill in that one face of the point is flat, and the other is beveled along the edges and has a slight bevel at the tip of the point. Drills are chipped on all sides. The gravers may have from one to five points on a single flake. The implements in this group range in size between one with a length of 19 mm, breadth of 13 mm, and thickness of 3 mm, and another with a length of 55 mm, breadth of 33 mm, and thickness of 6 mm. The actual graver points do not vary greatly in size. They consistently range between 1.5 and 2 mm in length and 1 and 1.5 mm in width at the base.

The chisel-gravers are more definitely shaped than the gravers. They are not as numerous, the type forming only 1 percent of the total collection, but they nevertheless are a distinct tool (pl. 9, *k, l, m*). They also were made from flakes. In contrast to the gravers, the points are broader and more elongated. There is a pronounced bevel on the tip, and the end of the latter is a straight edge, convex on rare examples, rather than a sharp point. These implements exhibit better workmanship than that on the simple gravers. The chipping is not confined to the points but as a rule extends along the edges, sometimes even around the base. The chisel-gravers range from 25 to 37 mm in length, from 13 to 27 mm in breadth, and from 3 to 8 mm in thickness.



The points range between 3 and 10 mm in length, from 4 to 7 mm in width at the base, and from 2 to 3 mm in width at the cutting end.

Both gravers and chisel-gravers are found in combination with other tools. There is a definite group of "snub-nosed" scrapers exhibiting the feature, and not a few side scrapers have one or the other type of point on a side or an end. Such specimens suggest that the small points may have served a utilitarian as well as an artistic purpose, although it is hard to postulate what such a function might have been. Most of them are too small to have served as awls or perforators.

#### CHOPPERS

Implements of this type are not numerous in the collection, comprising only 0.5 percent, but they form a definite class. They could be considered as variations of the tools generally called hand axes or rough celts (fig. 5, *a* and *b*). To avoid complications in the matter of correlation and chronological implications not necessarily justified, neither of those more common names will be used in referring to such objects. The choppers were made from true cores or from pseudo cores. The latter were originally flakes of more than average size which produced an object exhibiting in all respects the characteristics of a core implement despite the fact that the stone from which it was formed was not a complete nodule. The general shape of the tools suggests the adze or celt of the later Indians. The workmanship was not as good as that on the chipped celts of more recent times. The makers were apparently satisfied with the minimum expenditure of effort needed to make a usable tool. The main outlines were roughed out by the removal of large flakes, and the finer chipping was reserved for one chisel-like end. The bases are rough. As there is no trace of rubbing or polish on the stones to indicate that they were hafted, they may have been held in the hand. If so, the butt ends were probably wrapped in a piece of bison skin or similar substance to prevent slipping and to protect the user's palm.

The specimen marked *a*, figure 5, has an overall length of 71 mm. It is 43 mm wide at the base end and 27 mm wide at the cutting edge. The thickness at the base is 28 mm and at the bit 5 mm. Chopper *b*, fig. 5, has a total length of 74 mm. It is 39 mm broad at the base and 24 mm wide at the cutting edge. The base is 22 mm thick and the cutting end 3 mm.

Numerous unworked stones which were so shaped by nature as to make efficient choppers were found on the site. That many of these were used in splitting and hacking bones was suggested by the fact



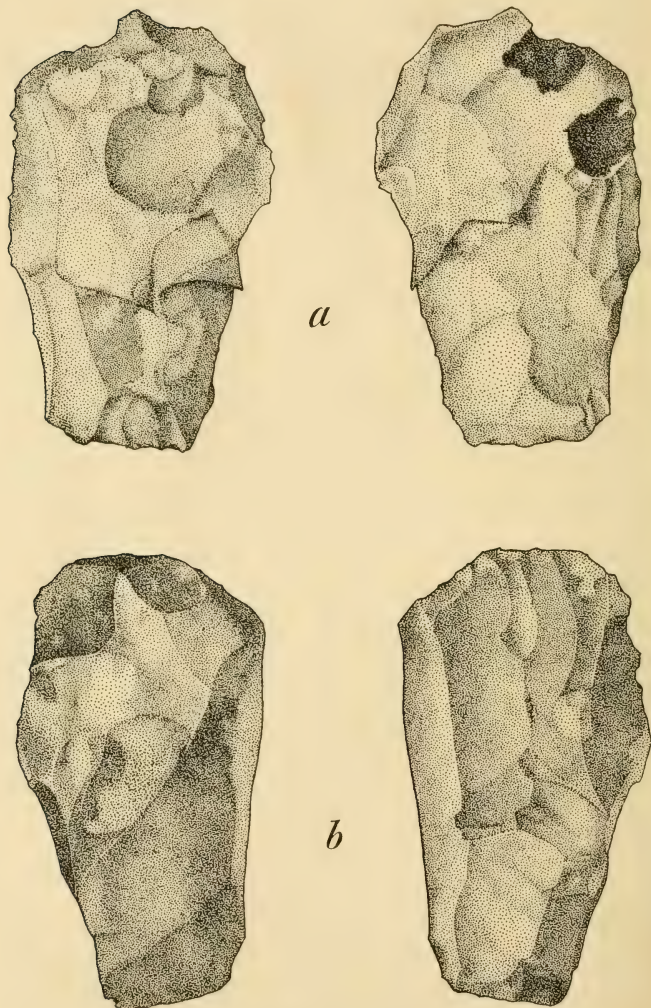


FIG. 5.—Choppers. (Actual size.)

that they were found in association with such objects. Several of these natural choppers also have slightly battered edges, showing that they had been employed as tools.

#### KNIVES

The specimens which may be grouped under the classification of knives consist of implements made from large, ribbonlike fragments of stone modified only by chipping along the edges; flakes which were more carefully shaped and bear a general resemblance to modern knife blades; and skillfully chipped stones which exhibit typical Folsom features in their fluted faces and secondary retouch along the edges. Tools in this group comprise 3 percent of the collection.

The ordinary flakeknives (pl. 10, *a-f*, and pl. 11, *a-c*) are crude implements, yet would be quite efficient in use. On some of them the chipping is large and irregular, on others (pl. 11, *a*, for example) it is as minute and precise as could be desired. Both convex and concave edges are present in the series. Some of the tools have two types on a single side, others on opposite sides. There is nothing to indicate that any of these cutting edges were hafted in handles, but it is quite possible that some of them were. The flakes range from 37 to 79 mm in length and from 10 to 45 mm in breadth. The thickness varies from 2 to 11 mm.

The group which shows more definite shaping (pl. 11, *d-f*) comprises specimens which exhibit some of the finest chipping noted in the collection. Not all of them were subjected to the same degree of workmanship, but the class as a whole is much superior in finish to the rough flakeknives. It seems probable that most of the blades in this group were hafted. All have an unfinished end, and on a few there is a slight gloss or luster such as a handle might produce. Measurements in this group range between 45 and 80 mm in length, 20 and 28 mm in breadth, and 3 and 8 mm in thickness.

The carefully chipped blades with fluted faces (pl. 10, *g* and *h*) comprise only 18 percent of the knives. So far as craftsmanship is concerned they are comparable in every way to the projectile points. The same technique was employed in their manufacture. Their ends, however, are rounded and blunt. In some cases they were smoothed. The cutting edges tend to be parallel rather than tapering or bulging as in the case of the points, yet such a knife could be converted into a typical point by the mere expedient of chipping the blunt end to a penetrating tip. These knives were undoubtedly mounted in a handle. Blades in this group range from 51 to 70 mm in length, 23 to 31 mm in width, and 4 to 6 mm in thickness.

Knives were also made from channel flakes, or perhaps it might better be said that channel flakes were used as knives. The razor-keen edge of these byproducts would be ideal for cutting purposes. Study of such flakes suggests that they were first employed as struck-off from the face of the point. Then as the edge became nicked and dulled in use it was touched up with the flaking tool.

#### LARGE BLADES

The tools and fragments from such implements classed under the heading of large blades are leaf-shaped objects which combine both the qualities of a knife and a scraper. This group constitutes 6.3 per cent of the series. These specimens are suggestive of the so-called blanks of later periods. The latter were the intermediate stage between the original nodule and the finished tool. They were roughed out in the quarry and then carried home to be completed as time permitted. The blades from the Lindenmeier site are actual implements, however, despite their similarity to the blanks. On many of them there is a careful secondary retouch along the edges. Others show minute chipping of the type which results from use. They would have functioned well in the skinning and cutting up of an animal and also in the scraping of a hide. Some of them exhibit a slight rubbing or gloss at the base which suggests the use of handles, while others do not. Even in an unhafted state they would be quite serviceable.

The blades range in size from 55 to 90 mm in length, 35 to 40 mm in width, and 7 to 9 mm in thickness. The majority fall between 75 and 80 mm in length, which might therefore be termed the standard length.

#### MISCELLANEOUS OBJECTS

Several varieties of specimens are grouped under this heading because they constitute only a minor part of the collection. In some cases there is only a single example of the class. Other objects are not actual tools or implements, yet are an integral part of the general complex. Included in this listing are the worked bones, channel flakes, hammerstones and rubbing stones, and pieces of hematite.

Only a few bones show signs of use or of having been shaped for some definite purpose. Many have cuts and marks made at the time when the flesh was stripped from them or when they were split for their marrow, but this is not considered indicative of workmanship preparing them for some special function. One difficulty in judging the bone material lies in the fact that most of it has been decalcified,

and an accompaniment of this phenomenon seems to be the sloughing of the outer surface. The surface is frequently essential in the identification of a fragment of bone as a tool. A number of chance scraps in the collection could have served as implements, but because the outer surface is gone, the polish acquired through use is missing, and for that reason it can not be stated with assurance that they were tools. Each of these specimens has a tapering, blunt-pointed end like that on punches and awls. Their sides have been rubbed and the base end is rounded, but because signs of usage are absent they cannot be designated as such tools. There is no question but that the people used bone implements, because the collection contains small fragments, preserved by having been charred in a fire, that exhibit the smooth and highly polished surfaces characteristic of awls. The pieces are too small, however, to give any clue as to the size and general shape of the specimens. Two pieces cut from the shaft of a long bone, each with one sharp, well-defined edge, would be serviceable as knives or fleshers. As green bone they would have functioned efficiently either in skinning or in scraping the fat and hair from a hide. The edges of both are slightly discolored and show a trace of polish. Another object suggests that it was the end of a paddlelike scoop. It also was cut from the shaft of a long bone.

The bone disk with ticked edges (pl. 9, *c*) has already been mentioned. This object was probably a marker or gaming die. It cannot be considered as an ornament in the strict sense of the word, as there is no perforation for suspension and no indication that it was attached to any other substance. It seems to have been fashioned from a piece of scapula or shoulder blade. Both faces are smooth, except for the series of cut lines bordering the circumference. This specimen and approximately half of one similar to it obtained by the Denver Museum party are the best examples of worked bone found at the Lindenmeier site. The disk measures 34 by 28 mm, and is 2 mm thick.

The channel flakes form an interesting series because they demonstrate so impressively the consummate skill of the men who struck them off from the sides of the points. The flakes are smooth on one side, the one that formed the groove in the face of the point, and flaked on the other. Some are paper-thin; others are as much as 2 mm thick. One good example from a white chalcedony point is 45 mm long, 13 mm wide, and 1 mm thick. It is unquestionably the complete spall from the channel. One piece of channel flake fits into the groove on one of the butt ends recovered from the site. This is the only example of the flake and the point thus far obtained. Many of the channel flakes were discarded when removed, but others, as men-



tioned in the discussions of the gravers and knives, were employed in some utilitarian fashion before being tossed aside. Every type of material observed in the points or fragments of points is represented in the channel flakes.

The hammerstones are as a rule merely nodules with battered ends. Any chance stone which could be held in the hand and used for striking seemed to answer the purpose, although in a few cases (pl. 12, *i*, for example) the stone was roughly shaped to an oval form. The majority were like *k*, plate 12, however. These objects were probably employed in knocking flakes off large nodules, for cracking bones, and other purposes where a striking implement would be required. Harder types of stone were used for this purpose, and the specimens in the collection are of granite, quartz, and petrified wood. The hammerstones range between 12 and 16 ounces in weight.

The pieces of sandstone in the collection show that they were used as rubbing stones. Many of them have distinctly flattened sides and ends (pl. 12, *a*, *b*, *d*). Some of them suggest the small hand stone used by the later Indians in grinding grain, nuts, and other materials, but no mortars or nether milling stones have been found, and it therefore seems that they must have had some other function. As most of the fragments of this type are stained with red pigment, it is possible that they were used to work color into a skin or some other substance. One of the stones (pl. 12, *c*) has a shallow concavity in one side and may have been a paint bowl. A similar specimen was found in the 1934 work. Neither indicates that it was a mortar in which pigment was ground. Both must have served merely as mixing bowls or palettes. One piece has a number of grooves or scratches in one side. These indicate that it was employed as a sharpening stone for touching up the ends of bone awls.

Many pieces of hematite were obtained from various places in the excavations. Some are very small, but others are sizeable nodules. The surfaces on all of them are smooth and striated from rubbing. One piece was shaped until it approximates a trapezoidal form. An attempt was obviously made to perforate it, as it was drilled on two sides, but the hole was not completed. The owner probably intended to suspend it on a thong either as a pendant or to prevent loss. Hematite was widely used by the later Indians both for the making of ornamental objects and as a source of paint. To judge from the numerous fragments in the present collection, Folsom man also found it a necessary component in his material culture complex.

## IDENTIFICATION OF BONES AND MOLLUSKS

A number of animals, in addition to the bison, are represented by the bones found at the Lindenmeier site. As mentioned in the discussion of the bison pit, Dr. Gazin has identified the remains of that animal as a form of *Bison taylori*, one of the extinct species. The other bones were submitted to Dr. Remington Kellogg, assistant curator, division of mammals, United States National Museum, who made the following identifications:

Fox, *Vulpes velox*.

Wolf, *Canis mubilus*.

Rabbit, *Lepus townsendii campanius*.

Pronghorn (Rocky Mountain antelope), *Antilocapra americana*.

The fox, wolf, and rabbit were represented in the material obtained in 1934, but the antelope was a 1935 addition. The bison is the only extinct animal in the group. There has been no change in the others from the time of the Pleistocene; hence they throw no light on the problem of the age of the site.

The invertebrate material was submitted to Dr. Horace G. Richards, research associate, New Jersey State Museum. The specimens and his identifications were checked by Dr. H. A. Pilsbry, of the Academy of Natural Sciences of Philadelphia. Dr. Richards found nine species represented in the mollusks. They are:

*Gastrocopta armifera* Say.

*Gastrocopta ashmuni* Sterki.

*Pupilla muscarum* (Linne).

*Pupoides inornatus* Vanatta.

*Pupilla sonorana* Sterki.

*Vertigo* sp.

*Valonia gracilicostata* Reinh.

*Succinea avara* Say.

*Zonitoides arborea* Say.

Seven of these species live in the region today. Two of them are considerably north of their present northern limits. *Gastrocopta ashmuni* Sterki has its present northern limits at Grand Canyon, Ariz., and southern and central New Mexico. The other, *Pupilla sonorana* Sterki, has a present northern limit of Mora County, N. Mex. According to Dr. Richards, this northern occurrence of the two species may indicate a warmer climate at the time of the deposition of the fossils.<sup>23</sup>

<sup>23</sup> Letter from Dr. Richards to the writer, Dec. 14, 1935.



## SUMMARY AND DISCUSSION

The 1935 investigations at the Lindenmeier site consisted of the digging of two large trenches through the area where objects attributable to Folsom man are found, of further excavations in the deep pit in the ravine bank where most of the specimens obtained during the preliminary investigations were dug, and of uncovering the remains of a group of bison at the location where Judge C. C. Coffin, A. L. Coffin, and Maj. Roy G. Coffin made their original discoveries. The collection obtained from the work contains some 750 specimens, large quantities of chipper's debris, and numerous bones from animals killed by the former occupants of the region. The artifacts comprise a series of tools and implements of which 11.3 percent are points, 32.8 scrapers, 5.6 graters, 1.0 chisel-graters, 0.5 choppers, 3.0 knives, 6.3 large blades, 0.8 hammerstones, 1.6 pieces of hematite which have been rubbed or shaped, 13.6 channel flakes from the longitudinal grooves in the faces of the typically fluted points, 4.0 sandstone rubbers, 0.5 pieces of bone showing evidences of workmanship, and 19 percent flakes showing signs of work but too nondescript in character to permit classification as types of implements. The artifacts as a group show that the lithic component in the local cultural pattern was primarily a flake industry, slightly less than 1.5 percent of the implements being of the core type.

The size range in the points in the collection raises a pertinent question, namely. On what type of weapon were they used? The general conception, based on knowledge of the Southwest and the Mexican area, has been that the bow and arrow was a late development in the New World and that older cultures employed a spear and spear thrower. Archeologists occupied with the Folsom problem have assumed that the fluted points, because of their size, were used in a shaft hurled from a spear thrower. Many of the smaller examples in the present group could easily have functioned as arrowheads and suggest that the early bison hunters may on occasion have used the bow. Definite conclusions should not be attempted solely on the evidence of stone points, but attention should be called to the fact that all of them are not necessarily of a size requiring a spear shaft.

Interesting evidence on one of the "burning issues" in the archeology of the western plains area, the Folsom-Yuma problem, was obtained from the investigations. Stratigraphic material demonstrated that as far as the Lindenmeier site is concerned there was only a very late contemporaneity between Folsom and Yuma points, the Yuma appearing toward the end of the Folsom occupation and surviving

longer. Furthermore, Yuma points constitute so small a factor that it is questionable whether they should be considered as belonging to the complex.

Five species of animals are represented in the bones from the site. Only one, the bison, is an extinct form. Nine species of mollusks were found and while none of these is extinct, two are considerably north of their present range. Their presence at the Lindenmeier site is considered an indication that the climate was somewhat warmer and moister when Folsom man was there than it is now.

The large trenches revealed in cross-section the deposits overlying the old level of occupation and demonstrated that what now constitutes a terrace was at one time an old valley bottom. The ridge that bordered its southern side has been eroded away since the area was abandoned by its aboriginal occupants. The nature of the valley fill, as exposed in the trench walls, suggests that the changes which culminated in the present state of the site could not have been extremely rapid ones. Considerable time must have elapsed since the layer containing the man-made objects was laid down. Evidence in the trenches also indicated that the makers of the tools and the Folsom points stopped for a time along the slope above the old valley bottom. If the trenches did not cross a portion of the real campsite, they at least bordered on it. This was shown by the finding of cut and burned bones, charcoal and wood ashes, hammerstones and chipper's debris, and implements broken in the making. All were so situated that their locations could not be attributed to drift or to the washing down of material from higher levels. The broken implements, when the fragments are fitted together and the original flake is restored, give good evidence of the technique used in the manufacture of tools.

The trenches did not produce data that are of aid in determining the age of the site. Despite their establishing the fact that the soil layer in which the objects are found was produced by the natural decay and break-up of the top of the Oligocene bed underlying the area, they gave no clue either to the agency that originally eroded away the overburden, thus laying bare the Tertiary stratum and forming the old valley, or to the time when the action took place. Conditions at the Clovis lake beds are somewhat better from the standpoint of dating, and Dr. Ernst Antevs has reached the conclusion, from extensive studies of the area, that the Folsom artifacts found there represent an antiquity of from 12,000 to 13,000 years.<sup>24</sup> Since the Clovis material indicates that it comprises the relics of a people whose material

<sup>24</sup> Antevs, 1935, p. 311.

culture was similar to that of the group occupying the Lindenmeier site, it may be suggested that the latter was approximately the same age. This should not be regarded as an established fact; it is merely a postulation based on analogy. Subsequent work may show the two sites to have been as widely separated in time as they are in space. There is still an opportunity to obtain a geologic date for the Lindenmeier site through a study of the terrace system of the South Platte River and the relation of its terraces to the glaciation in the Rocky Mountains to the west. The Lindenmeier terrace can be correlated with those of the South Platte, but as yet there has been no determination of the ages of the latter. An attempt to solve this particular problem will constitute a part of the program for future work in the region.

No human remains have been found, and so far as his physical characteristics are concerned, Folsom man is still a *persona incognita*. There is no evidence as to what type of shelter he may have used. On the other hand it seems obvious that he was a typical hunter depending entirely upon the bison for his maintenance and sustenance. He no doubt supplemented his preponderant meat diet with wild seeds and "greens" but did not cultivate his own vegetal food. He probably did not settle long in one place but traveled wherever the bison moved, in order to support himself. For that reason it is not likely that his dwelling consisted of anything more substantial than a tent made from the skins of that animal. Traces of the places where he pitched his shelter will be extremely hard to find at this late date. A hard packed floor and hearth, perhaps some post molds, is the most that can be expected. He probably tarried as long at the Lindenmeier camp as he did at any of his settlements, possibly longer than at most of them when its advantages are recalled. Hence the chances of locating a lodge site or even of uncovering his own remains are not altogether beyond the bounds of likelihood.

The old valley bottom with its numerous meadows, marshes, and bogs undoubtedly attracted bison because of the reeds and sedge grasses for feed and the mire in which to wallow. It is not likely that large herds frequented the district—rather that small groups drifted in from the plains to the east. The presence of the animals would draw Folsom man into the area, but in addition there were the assets of raw material for use in making implements, a good supply of water, firewood, and a pleasant camping spot. Here he could stalk his game, cut and dry the meat not wanted for immediate consumption, tan the skins, make his tents and such clothing as his needs required, fashion

his tools from the available stone, and prepare his equipment for the inevitable trek when the bison shifted to other pastures.

Present indications are that the Lindenmeier site was not occupied continuously by a large group of people. It probably was an annual summer and fall camping grounds visited regularly over a period of years by smaller parties. That the intervals between occupations were not protracted is shown by the homogeneous nature of the layer in which the artifacts are found.

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1. GENERAL VIEW OF SITE SHOWING RAVINE AND TRENCHES  
ACROSS TERRACE



2. LOWER END OF TRENCH A  
Man standing on top of clay substratum.





1. SIFTING EARTH FROM SECTION AT LOWER END OF TRENCH A



2. ARTIFACTS IN SITU

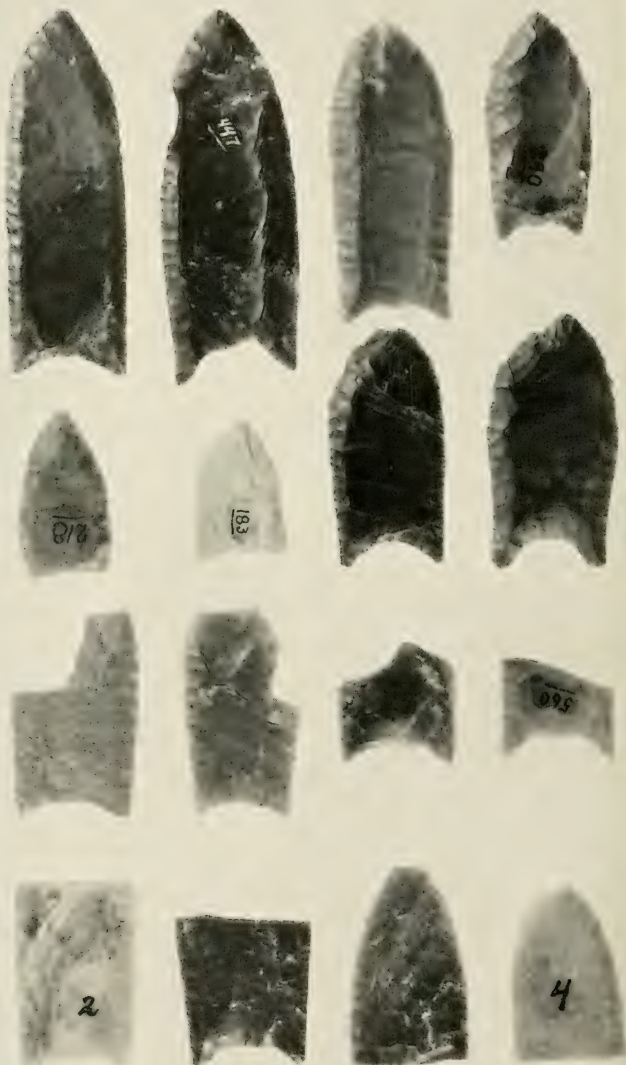
Chopper at left, portion of Folsom point at right.



1. UNCOVERING ARTICULATED BISON LEG IN BISON PIT



2. VERTEBRA WITH POINT IN VERTEBRAL FORAMEN



FOLSOM POINTS

Actual size.



*a*



*b*



*c*



*d*



*e*

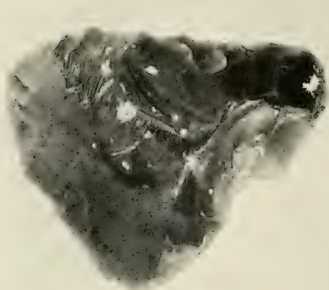


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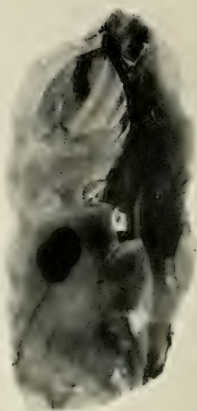


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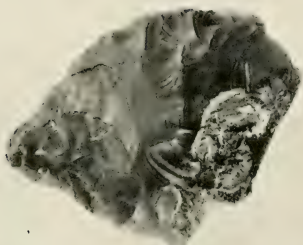
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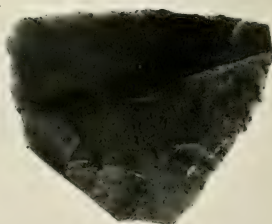
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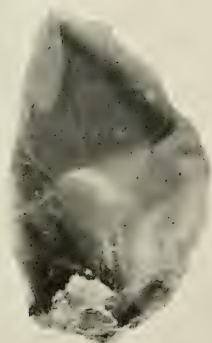
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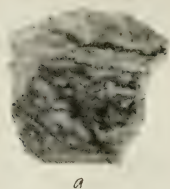




LARGE QUARTZITE SCRAPERS

One-half size.

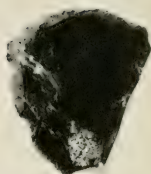




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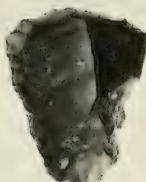
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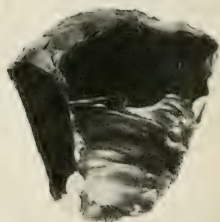
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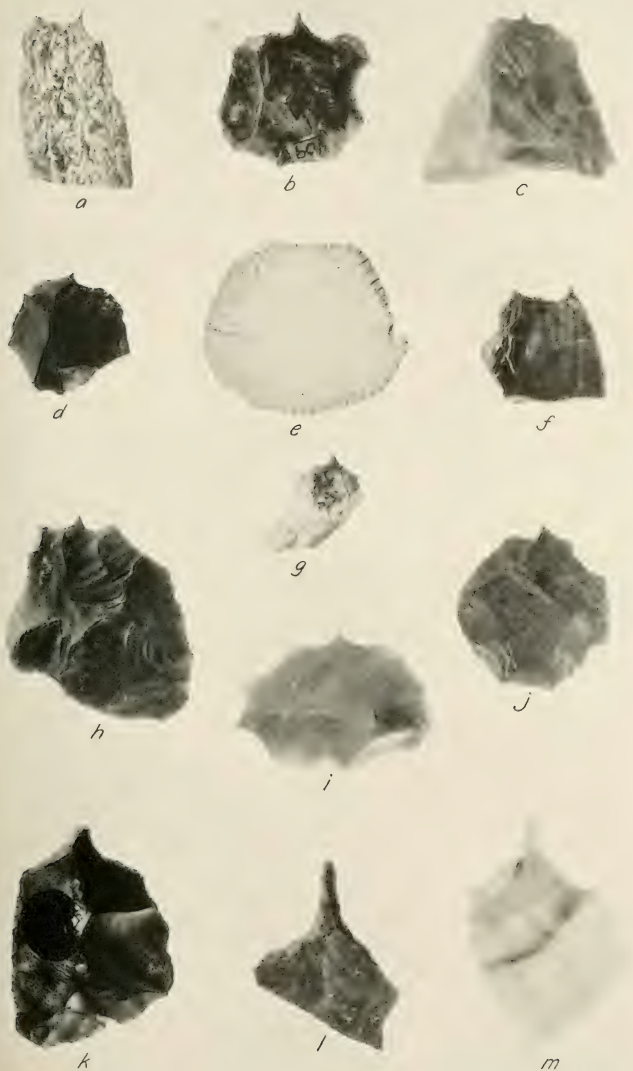
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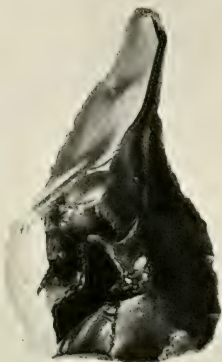


GRAVERS, CHISEL-GRAVERS, BONE DISK

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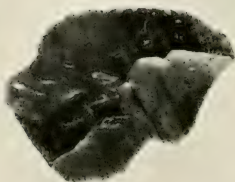
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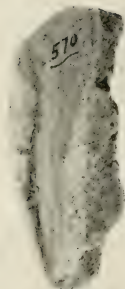
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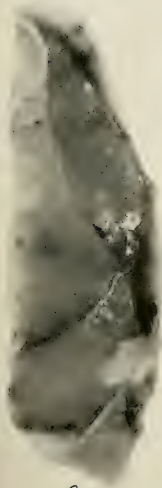
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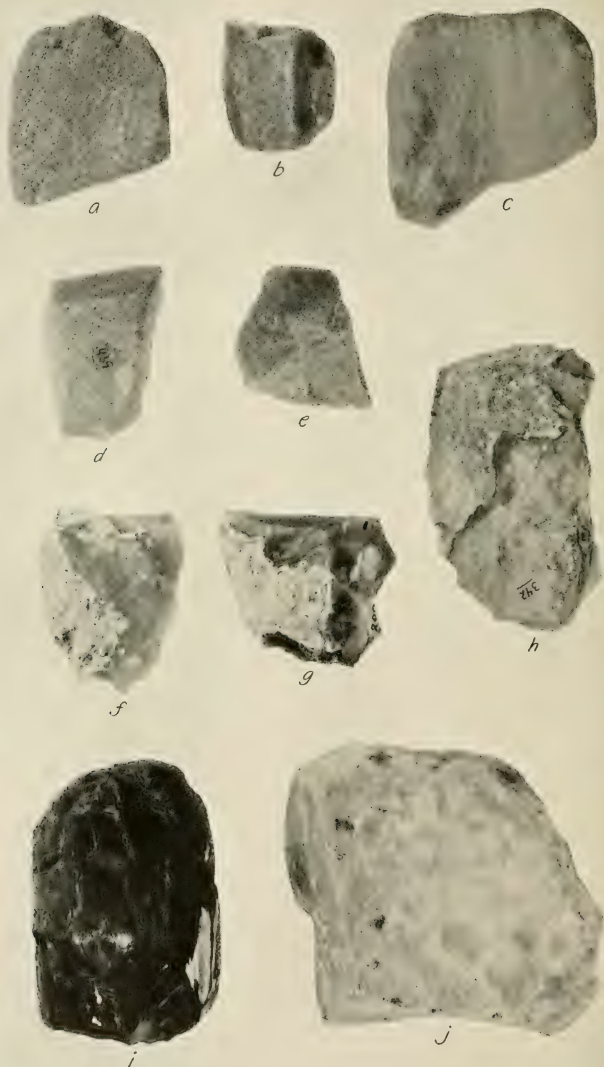


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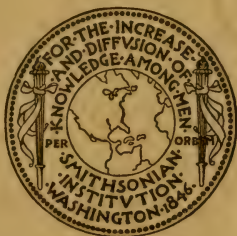
RUBBING STONES, A-E; SCRAP NODULES, F-H; HAMMERSTONES, I-J  
One-half size.

SMITHSONIAN MISCELLANEOUS COLLECTIONS  
VOLUME 95, NUMBER 11

## Arthur Fund

# INFLUENCE OF PLANETARY CONFIGURATIONS UPON THE FREQUENCY OF VISIBLE SUN SPOTS

BY  
FERNANDO SANFORD  
Palo Alto, California



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PRINTED AT THE CITY OF WASHINGTON  
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### INFLUENCE OF PLANETARY CONFIGURATIONS UPON THE FREQUENCY OF VISIBLE SUN SPOTS

BY FERNANDO SANFORD

*Palo Alto, California*

In any discussion of sun-spot frequency it should be borne in mind that only one-half of the Sun is visible to us at one time, and that all sun-spot data refer only to spots on the terrestrial side of the Sun.

In 1907 A. S. D. Maunder published a paper entitled "An Apparent Influence of the Earth on the Numbers and Areas of Sun-spots in the Cycle 1889-1901."<sup>1</sup> Mrs. Maunder found that for the years under consideration more spots came into view around the east limb of the Sun than passed out of view around the west limb; that is, that more spots died out on the visible side of the Sun than were formed on it. As a summary of Mrs. Maunder's observations we have the following table:

Spots born on visible hemisphere.....	384
Spots born on invisible hemisphere.....	572
Spots died on visible hemisphere.....	564
Spots died on invisible hemisphere.....	402

All told, 947 groups came into view around the east limb or formed close to it, and only 777 groups passed around the west limb or dissolved close to it. This leaves a difference of 170 groups, or 22 per cent of the disappearances, which seem to be due to some influence exerted by the Earth. Apparently, the Earth exerts an inhibitive influence upon the formation of sun spots upon its own side of the Sun or aids their formation upon the opposite side, or, perhaps, both. This plain inference seems not to have been tested in the case of other planets.

It is reasonable to infer that whatever influence the Earth may have on sun spots, a similar influence may be exerted by the planet Venus, which is comparable in size and mass to the Earth and is less than

<sup>1</sup> Monthly Not. Roy. Astronom. Soc., May 1907.

three-fourths the Earth's distance from the Sun. If such should prove to be the case, the visible spottedness of the Sun should be decreased when Venus and the Earth are on the same side of the Sun, or increased when they are on opposite sides, or both phenomena should appear.

In the publications of The International Astronomical Union are given the daily values of the sun-spot relative numbers beginning with 1917. The mean synodical period of Venus is 584 days. The daily sun-spot numbers for 10 synodical periods of Venus, beginning at superior conjunction of Venus and the Sun on April 25, 1917, and ending June 29, 1932, were arranged in regular order in their respec-

TABLE I

Superior conjunction						Inferior conjunction					
Apr. 25, 1917	103	88	104	102	96	29	24	26	20	67	Feb. 9, 1918
Nov. 20, 1918	187	127	135	80	107	47	53	65	53	53	Sept. 12, 1919
July 3, 1920	38	38	40	46	41	50	41	47	37	28	Apr. 22, 1921
Feb. 8, 1922	17	42	30	27	34	0	0	0	0	0	Nov. 24, 1922
Sept. 9, 1923	19	33	22	23	10	13	14	26	34	32	July 1, 1924
Apr. 24, 1925	44	36	30	31	26	34	29	35	44	32	Feb. 7, 1926
Nov. 21, 1926	20	53	101	112	113	40	44	47	68	92	Sept. 10, 1927
July 1, 1928	131	121	124	130	128	50	58	62	57	47	Apr. 20, 1929
Feb. 6, 1930	111	117	110	111	82	57	63	66	68	48	Nov. 22, 1930
Sept. 8, 1931	14	15	18	13	24	26	31	22	24	21	June 29, 1932
Sum. ....	684	670	714	675	661	346	357	396	405	420	

Average value at superior conjunction, 681.

Average value at inferior conjunction, 385.

tive periods and their average values for the 10 synodical groups were determined. The actual values for 5 days, 2 days before and 2 days after the day of conjunction, for the 10 superior conjunctions and the 10 inferior conjunctions of the 5,840 days under consideration, are given in table I.

It will be seen from the above table that the sun-spottedness was 76.9 percent greater when Venus and the Earth were on opposite sides of the Sun than when they were on the same side. In the actual days of conjunction this difference is 80 percent.

During the 10 synodical periods of Venus there were 20 days when Venus and the Earth differed in heliocentric longitude by 90 degrees. Five days were taken at each of these periods—2 days before and 2 after the exact day on which Venus and the Earth were

at an angular distance of 90 degrees—and the sun-spot numbers for each of these 100 days are given in table 2.

TABLE 2.—*The Earth and Venus at an angular separation of ninety degrees*

Sept. 18, 1917	97	119	140	149	182	Sept. 15, 1925	20	29	41	58	38
July 3, 1918	99	101	115	146	142	July 1, 1926	111	109	104	76	79
Apr. 2, 1919	16	25	33	29	58	Apr. 16, 1927	138	131	157	124	120
Feb. 6, 1920	22	26	22	30	31	Feb. 4, 1928	50	65	41	46	34
Nov. 26, 1920	24	47	42	35	33	Nov. 24, 1928	28	33	16	7	29
Sept. 15, 1921	26	23	35	29	26	Sept. 13, 1929	39	31	53	25	32
July 2, 1922	0	0	0	0	0	June 19, 1930	16	15	9	14	8
Apr. 17, 1923	0	0	14	13	7	Apr. 16, 1931	38	37	31	41	22
Feb. 3, 1924	0	0	0	0	0	Feb. 2, 1932	17	19	16	17	8
Nov. 26, 1924	53	54	46	33	23	Nov. 24, 1932	12	0	0	0	0
Sum.....	337	395	447	464	502		469	469	468	408	370

The mean sun-spot number for the 100 days of the above table is 43.29, whereas for the 50 days near superior conjunction it was 68.1 and for the 50 days near inferior conjunction it was 38.5.

It would appear from these results that the influence of Venus on visible sun-spottedness is much greater when the planet is on the opposite side of the Sun from the Earth than when it is on the same side as the Earth. That is, the apparent effect of Venus upon sun spots is to repel them to the farther side of the Sun. The phenomena observed by Mrs. Maunder indicate that the Earth also apparently repels sun spots to the farther side of the Sun.

In the case of Mercury and the Earth, the eccentricity of the elliptical orbit of Mercury is so great that the distance of the planet from the Sun is more than 1.5 times as great at aphelion as at perihelion. It seems probable that the distance of Mercury from the Sun must influence whatever effect it may have on total sun-spottedness, and its position relative to the Earth must influence the visibility of these spots.

The period of sidereal revolution of Mercury is 88 days. Its synodical period is 116 days. Accordingly, superior conjunction with the Sun will occur every 116 days, and perihelions will be 88 days apart. If we assume that both of these positions are favorable to the production of visible sun spots, their resultant influence is very hard to determine. Also, Mercury moves in its orbit 2.3 times as fast at perihelion as at aphelion, and is 33 days on the perihelion side of the Sun and 55 days on the aphelion side.



Taking the above facts into consideration along with the known disturbing influence of Venus, it seems, if not hopeless, yet very difficult to detect with certainty any effects of the relative positions of Mercury and the Earth upon the visible spottedness of the Sun.

Nevertheless, the sun-spottedness of 20 periods of 116 days each, starting from the inferior conjunction of Mercury and the Sun, were added and their mean sun-spot numbers were represented graphically. The resulting curve was very irregular and gave no plain indication of a marked sun-spot activity at either conjunction. However, in the twenty 116-day periods the sun-spot numbers at inferior conjunction averaged 48, and on the 58th day after inferior conjunction they averaged 57, showing an increase of about 15 percent when the Earth and Mercury were on opposite sides of the Sun.

It seems unwise to lay too much stress upon this one set of observations. A very large number of such series taken at widely distributed intervals would be necessary to determine with certainty the influence upon visible sun spots of the relative positions of Mercury and Earth.

An attempt was made to determine whether there is an appreciable difference in sun-spottedness as seen from the Earth when Venus and Mercury are on the same, or on opposite, sides of the Sun. Twenty-two groups of 5 days each were taken when Venus and Mercury were at the same heliocentric longitude, and the mean value of the sun-spot numbers for the 110 days so taken was 35.4.

Twenty-three groups of 5 days each, covering the same period taken when the heliocentric longitudes of Venus and Mercury differed by 180 degrees, gave a mean value for the sun-spot numbers of 44.2 for the 115 days.

Forty-four groups of 5 days each, covering the same period, were taken when the heliocentric longitudes of the planets differed by 90 degrees. The mean value of the sun-spot numbers for these 220 days was 38.5.

The mean value of the observed sun-spot numbers when the planets were on opposite sides of the Sun was 24.9 percent greater than when they were on the same side. The observed spottedness when the planets were at an angular separation of 90 degrees was 8.8 percent greater than when they were on the same side of the Sun and 12.9 percent less than when they were on opposite sides of the Sun.

The above data do not take into consideration the relation of either planet to the Earth during the period under consideration, and it seems probable that a similar set of data taken at a different time would show different results. Nevertheless, they seem significant and are given for whatever they are worth.

Similar comparisons were made with Mars and the Earth and with Jupiter and the Earth and with the two planets taken together. In all cases the observed effects were virtually inappreciable, being less than 3 percent in every case.

From the above data it seems safe to assert that sun spots are influenced by the configurations of Venus and the Earth and probably by Mercury and the Earth, and Mercury and Venus. In the case of the other planets no such effect has been shown.

In the foregoing discussion no attempt has been made to propose any theory of the formation of sun spots. It has merely been shown that sun spots are as if repelled by the Earth and the nearer planets. Any sun-spot theory must account at least for this effective repulsion.

In spite of the prevailing opinion of astronomers as expressed by Stratton in "Astronomical Physics" that enormous electric fields in and near the Sun "must be ruled out," it seems to be universally agreed that the rotating gases which give rise to the powerful magnetic fields of sun spots are highly electrified.

The only known body which can repel an electrically charged body is another body similarly electrified. If the planets which are known to repel the charged sun spots are themselves electrified in the same manner as the repelled sun spots, we have a probable explanation of this repulsion.

Whether the planets are so charged or not is a purely qualitative question which cannot be answered by any mathematical theory, but only in the same manner that we may determine the electrification of any insulated body, namely, whether it repels or attracts a known electrified body and whether its rotation may generate a magnetic field.

The author has shown in his monograph on "Terrestrial Electricity"<sup>2</sup> that the Sun, the Earth, and the Moon have all given what seems to him conclusive proofs of their negative electrification. If this should be suspected in the case of the other planets, it only remains to inquire what other phenomena which have been observed between electrified bodies may be detected between the planets and the electrified gases of the Sun.

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<sup>2</sup> Sanford, Fernando, *Terrestrial Electricity*, Stanford University Press, 1931.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 12

## Arthur Fund

# THE DEPENDENCE OF TERRESTRIAL TEMPERATURES ON THE VARIATIONS OF THE SUN'S RADIATION

BY

C. G. ABBOT

Secretary, Smithsonian Institution

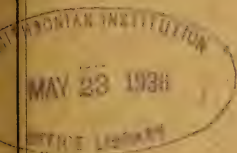


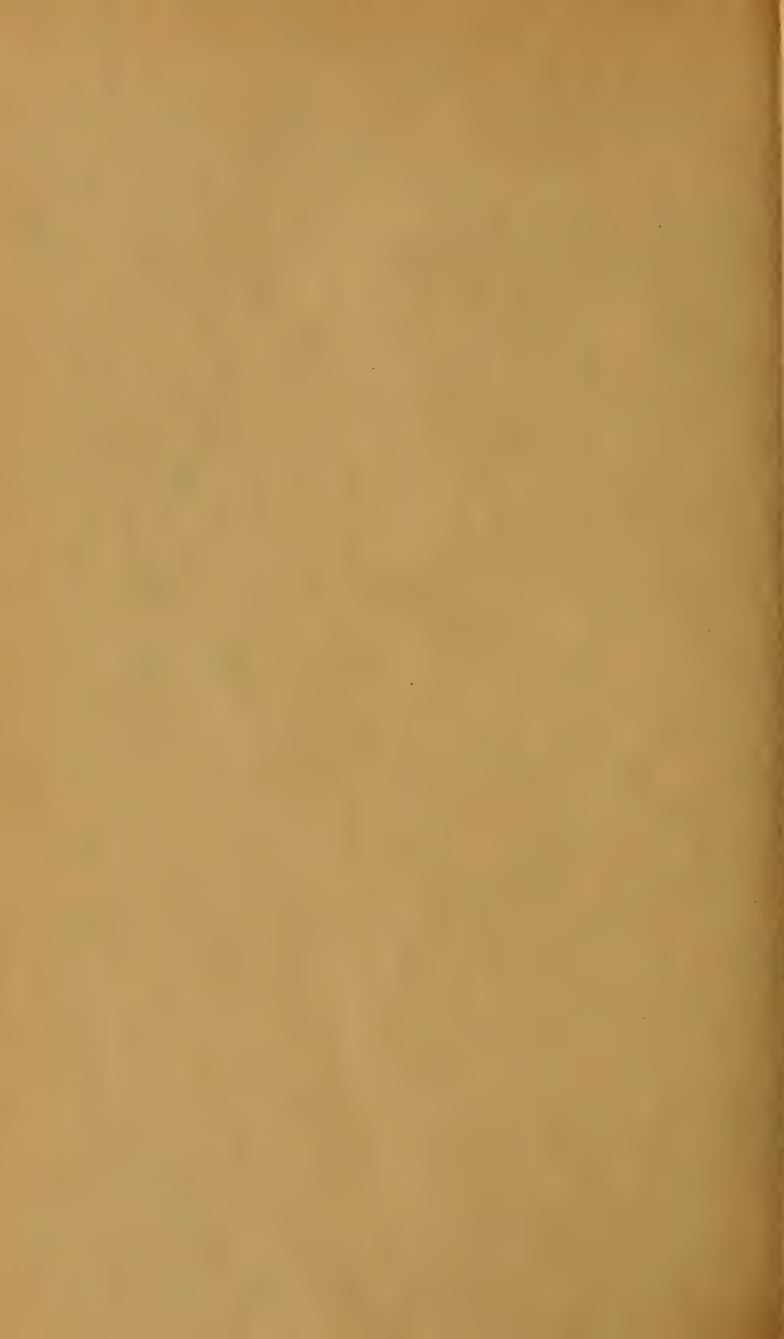
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MAY 23, 1936





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*Secretary, Smithsonian Institution*

The burden of this paper is an affirmative answer to two questions: 1. Does the variation of the sun's radiation sensibly affect the course of temperature in terrestrial weather? 2. Conversely, does the march of terrestrial temperature support the view that the sun is a variable star?

As long ago as 1920 Clayton expressed his affirmative conclusions as to these questions in a paper<sup>1</sup> published by the Smithsonian Institution. I introduced Clayton's paper of 1920 with a note, from which I shall quote at the end of this discussion several paragraphs still pertinent, including the text figure which accompanied my note as the frontispiece of Clayton's paper. I returned to the same subject in 1931 in my paper<sup>2</sup> "Weather Dominated by Solar Changes", in which I employed solar observations made at Montezuma, Chile, 1924 to 1930, in relation to the temperature departures at Washington and other stations. I am now able to present the results of 5 more years of solar study, with a revision of the work published in my paper of 1931.

By a more discriminating scrutiny of the solar data I have eliminated some doubtful cases of solar change in the period 1924 to 1930, formerly included. Unfortunately, the solar radiation cannot yet be determined from a single day of observation with an accuracy better than about 0.3 percent. Hence, it is only by a well-supported series of quite a number of successive days' values of high apparent reliability, trending steadily in a given direction, that we may be well assured that a real and not an accidental indication of solar change is before us.

In volume V of the *Annals of the Astrophysical Observatory*, table 31 gives a long series of Montezuma measurements of the "solar

<sup>1</sup> Smithsonian Misc. Coll., vol. 71, no. 3, 1920.

<sup>2</sup> Smithsonian Misc. Coll., vol. 85, no. 1, 1931.

constant" of radiation ending with the year 1930. Similar measurements, as yet mostly unpublished, have been continued till the present time. Some of them have been broadcasted daily through Science Service, but they are not yet to be regarded as definitive until their further comparison and adjustments with results of other observing stations is completed. Nevertheless, they will serve for our present purpose.

This study relates to the daily departures from normal temperatures at Washington, D. C., St. Louis, Missouri, and Helena, Montana. These departures have been computed as follows: The general means of monthly averages of maximum and minimum thermometer for many years are used as printed on pages 956, 922, and 861 of World Weather Records (Smithsonian publication no. 2913). These monthly values, treated as representing the middle days of the months, were plotted on an adequate scale. Daily values were read from the smooth curves. The departures from these daily normals were then obtained for all days from January 1, 1924, to January 31, 1935, by subtraction from the current United States Weather Bureau Reports.

In order to fix the dates when sequences of rising and of falling solar emission of radiation occurred, Montezuma solar-constant values were used. As it was intended to segregate the investigations of each of the 12 months of the year separately, 12 solar-constant plots were made, each of which contained all of the values observed within a given month in all the years 1924 to 1935. Values of small weight were given the symbol "U" to identify them, and apparent sequences depending largely on such days were rejected.

That the reader may see how incomplete the record is, even from so fine a station as Montezuma, I give in figure 1 the plots for January and for April. It is believed that the reader will appreciate how hard it is to decide which are the satisfactory cases of rising and of falling sequences of solar change. After much scrutiny of the plots, the following dates were selected as zero dates of solar changes.

Before presenting the associated temperature departures for Washington, St. Louis, and Helena, attention is drawn to four criteria which should hold if solar variation really affects terrestrial temperatures.

1. Since opposite causes generally produce opposite effects, whatever curves may represent the average courses of the temperature departures following rising solar sequences, they should be opposite, as the right hand is to the left, to the average curves representing the after effects of falling solar sequences.

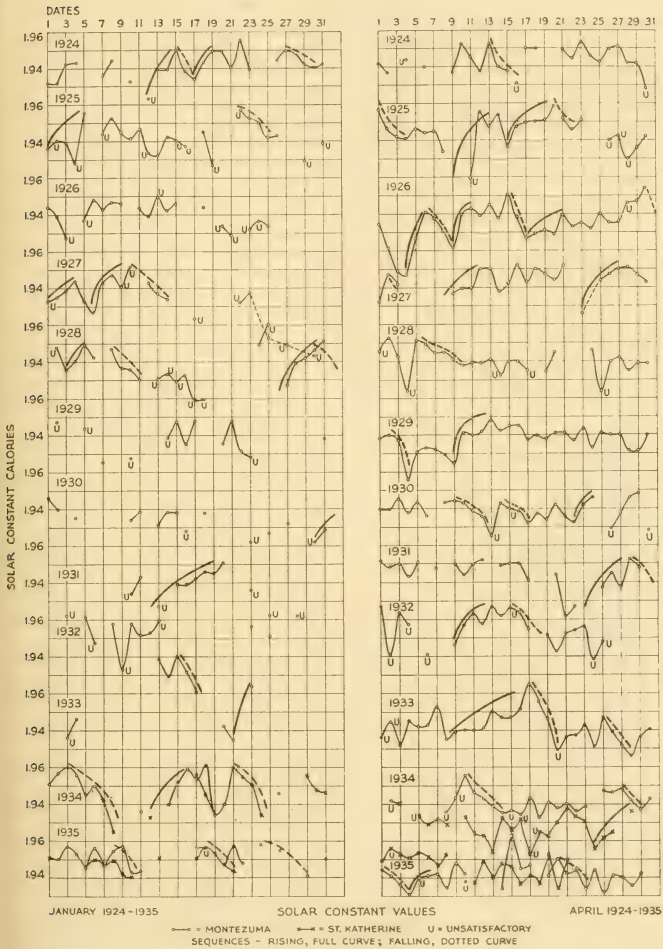


FIG. 1.—Incompleteness of available data indicating solar variation.

TABLE 1.—*Sequences of Solar Radiation Change*  
 Dates when sequences commenced

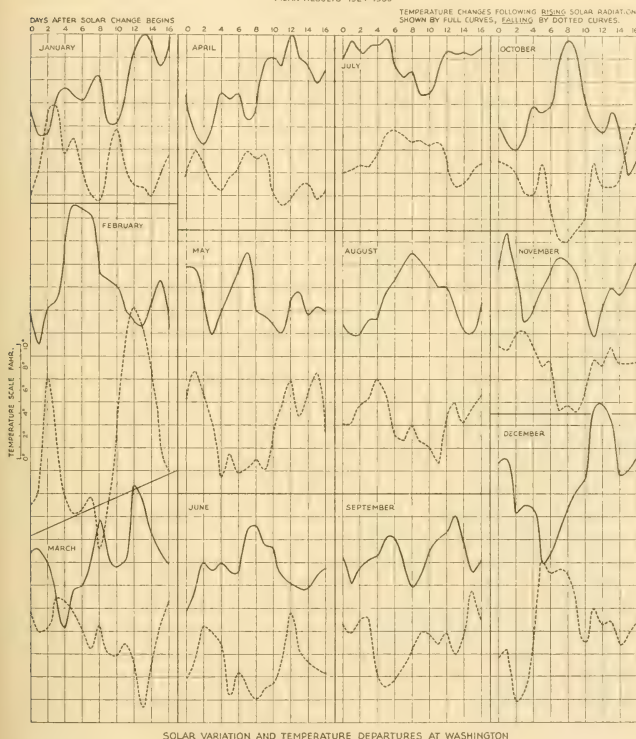
Year		1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	Total number cases
Month														
Jan.....	{ Rising { Falling	12, 17 15, 27	1 20	.. ..	1, 6 10	3, 26 8, 30	.. ..	30 ..	12 ..	.. ..	21 15	12 3, 22	26 <sup>a</sup> 8, 18, 24	12 12
Feb.....	{ Rising { Falling	5, 28 ..	.. ..	.. ..	8 ..	.. ..	4, 22 ..	.. ..	12 15	6 15	.. ..	8, 26 20	.. ..	9 3
Mar.....	{ Rising { Falling	.. 4	.. 16	8 30	29 26	5, 17, 24 9, 20	14 24	20, 30 16, 25	11, 28 15	5 ..	.. ..	.. 6	.. 19	11 12
Apr.....	{ Rising { Falling	.. 13	9, 15 1, 20	4, 9, 17 6, 15, 30	8, 23 2	.. 5	9 2	22 9, 14	23 28	9 15	8 17, 25	24 10, 27	4 1, 20	14 19
May.....	{ Rising { Falling	13 ..	4, 16 9, 21	5, 12, 20 2, 22	25 21	4 21	.. 4, 14	16 22	16, 26 22	.. ..	14 3, 12, 22	28 ..	7, 13 ..	15 13
June.....	{ Rising { Falling	13 ..	17, 30 26	.. ..	15 8	.. 7, 22	5, 12 ..	22, 27 24	23 ..	.. ..	2 8, 18	8 ..	20 12, 18, 25	12 10
July.....	{ Rising { Falling	12, 25 15, 22	23 9, 21	5, 29 12	15, 22 25	5 2, 7, 17	6, 18 2, 24	5, 10, 28 1, 15, 25, 30	.. 9, 22	.. 8	.. 24	2, 23 10	19 22	16 21
Aug.....	{ Rising { Falling	14, 23 4, 16	24 10, 22	25 27	23 18, 30	28 5	6 10, 20	18 ..	7, 23 11	.. 9	3, 21 5	3, 15, 29 20	5 14	16 14
Sept.....	{ Rising { Falling	1, 24 11, 19	14 5, 18, 30	12 7	12 22	29 20	12, 27 ..	10 1	25 14	9 11	11 9, 28	1, 19, 30 15, 20	9, 15 12, 29	17 17
Oct.....	{ Rising { Falling	18, 25 ..	.. ..	6 13	.. 10	9 ..	5 2, 16	8 15	.. 4	16 8, 21	25 17	13 6	23 ..	10 10
Nov.....	{ Rising { Falling	1, 6 10, 20	15 ..	.. 6, 13	11, 28 ..	17, 26 20	5 3	14, 23 10, 19	3, 14, 28 9, 17	11, 29 8, 19	6 3	22 5, 18	4, 12 8, 23	19 17
Dec.....	{ Rising { Falling	6, 23 2, 12, 22	9 4	.. ..	.. 7	.. 5	18 22	10, 23 14	.. 6, 13	14 17	.. ..	5, 13 11, 20	.. ..	9 12

<sup>a</sup> This date erroneous, but is included in the mean values and plots, having been discovered too late to correct. Its omission would have improved the general agreement.

2. Since greater causes generally produce larger effects, exceptionally wide ranges of solar variation should be associated with larger temperature ranges than the average of all the cases.

3. Since similar causes generally produce similar effects, the average results found in the years 1924 to 1930 should closely resemble

## MEAN RESULTS 1924-1935



SOLAR VARIATION AND TEMPERATURE DEPARTURES AT WASHINGTON

FIG. 2.—Oppositeness of temperature departures at Washington which follow average rising and falling sequences of solar variation.

in phases, though not necessarily in amplitudes, the average results found in the years 1931 to 1935.

4. Since the sun shines on the whole earth, temperature effects which fulfill criteria 1, 2, 3 should be found at all stations.

I will give first the results obtained with Washington temperatures. Figure 2 will show to what a high degree criterion no. 1 is



fulfilled at Washington. Certain months, as January, March, April, October, seem to be nearly unexceptionable as regards oppositeness of features. Yet for several reasons it must not be counted as a great blemish that some of the months are less perfect examples than these. First, it is clear from figure 2 that the temperature effects, if attributable to solar changes, continue for many days after the assumed solar causes have died away. Hence, each individual case of the many whose averages are plotted in figure 2 must probably have differed decidedly from the average during its individual course because the effects of previous or immediately succeeding solar changes were still incomplete. Only in the mean of a very large number of cases, many more than the 10 to 20 of each group going to form the averages, could these vestiges of effects of previous or succeeding solar changes be totally eliminated. Second, the arrangement of results by months is arbitrary. The proper arrangement would be according to the general meteorological condition prevailing in the Northern Hemisphere. Since there are wide differences between the curves in different months, it is highly probable that the cases which are forced together by the monthly classification should not, in fact, all go together under a proper classification. Third, owing to errors in solar-constant determinations, there is no doubt that some of the solar sequences referred to in table 1 are spurious. Hence, on these three accounts it ought not to be expected that every pair of curves in figure 2 should be precisely in opposition at all points.

Figure 3 gives the mean of April results at Washington for the years 1924 to 1930. Heavy lines give the general averages corresponding to rising and falling solar sequences respectively. Light lines give the averages of the two or three cases of each sort when rising and falling solar sequences well above the average in amplitude were observed. It will be seen that the ranges of these thin-lined curves are much greater than those of the thick-lined curves representing the general averages. Thus criterion no. 2 is supported. To add to its support, a tabulation was made of 150 cases in total to show the average ranges compared to the ranges of the 46 cases among them which presented exceptionally large solar sequences. The comparison showed average amplitudes in the ratio 1 to 1.95.

As for criterion no. 3, figure 4 gives the results for rising and falling sequences in the years 1924 to 1930 as compared to the years 1931 to 1935. The reader must again be cautioned as above not to forget the influences of continuing effects of preceding and immediately succeeding solar changes, of unsuitable classification, and of

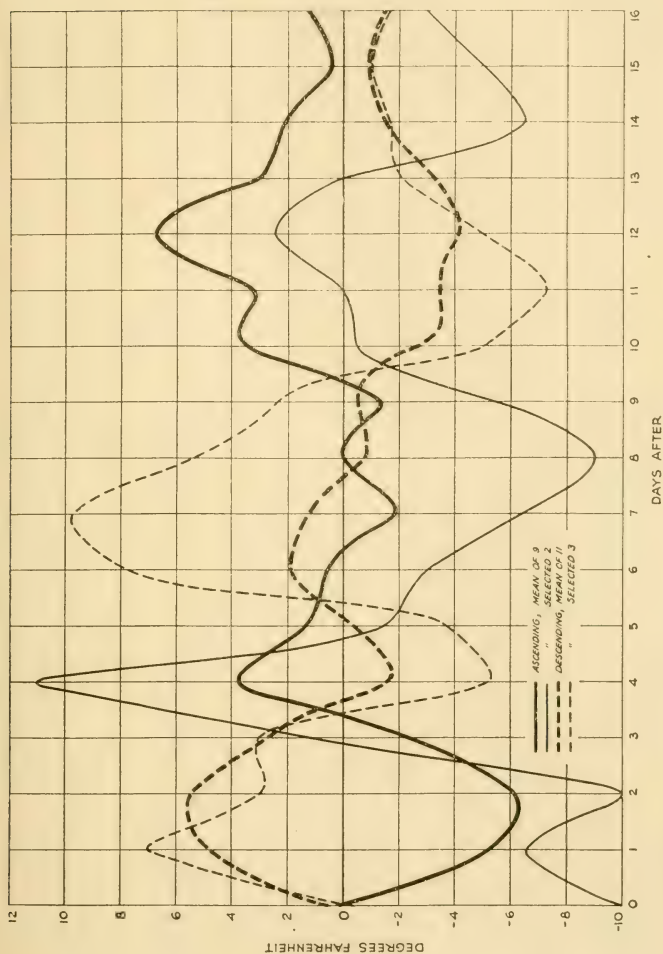
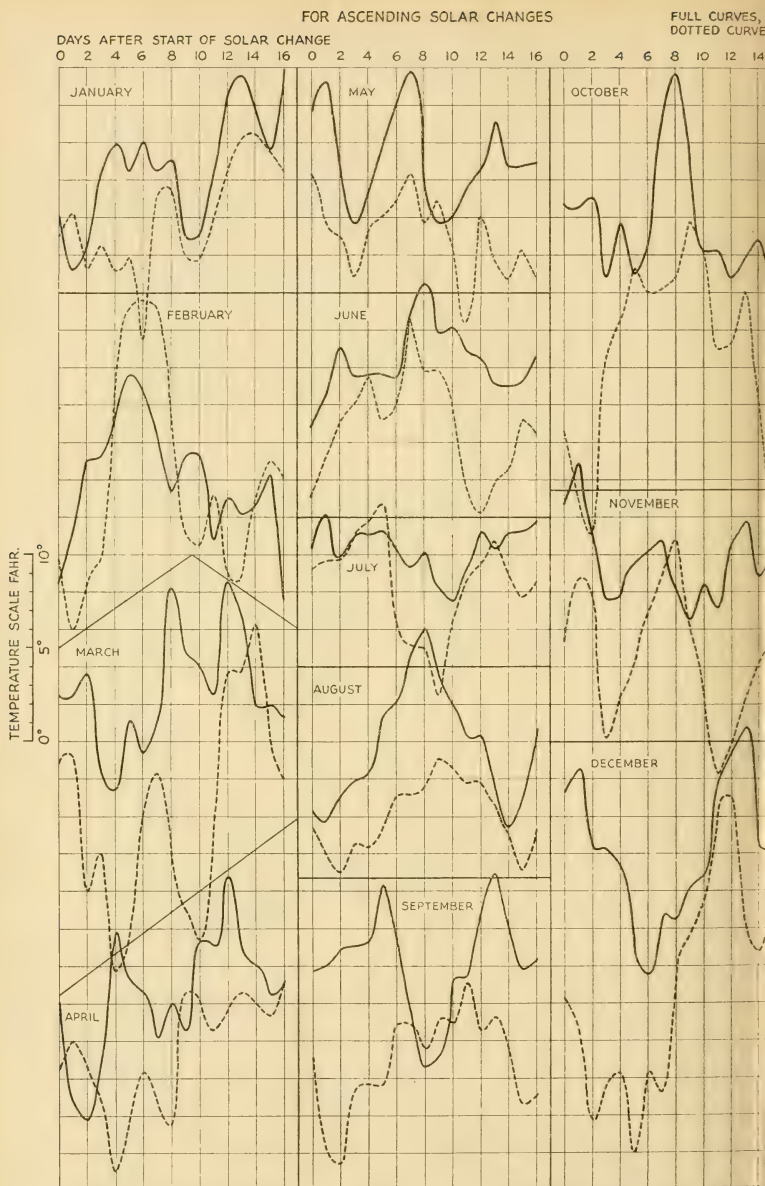


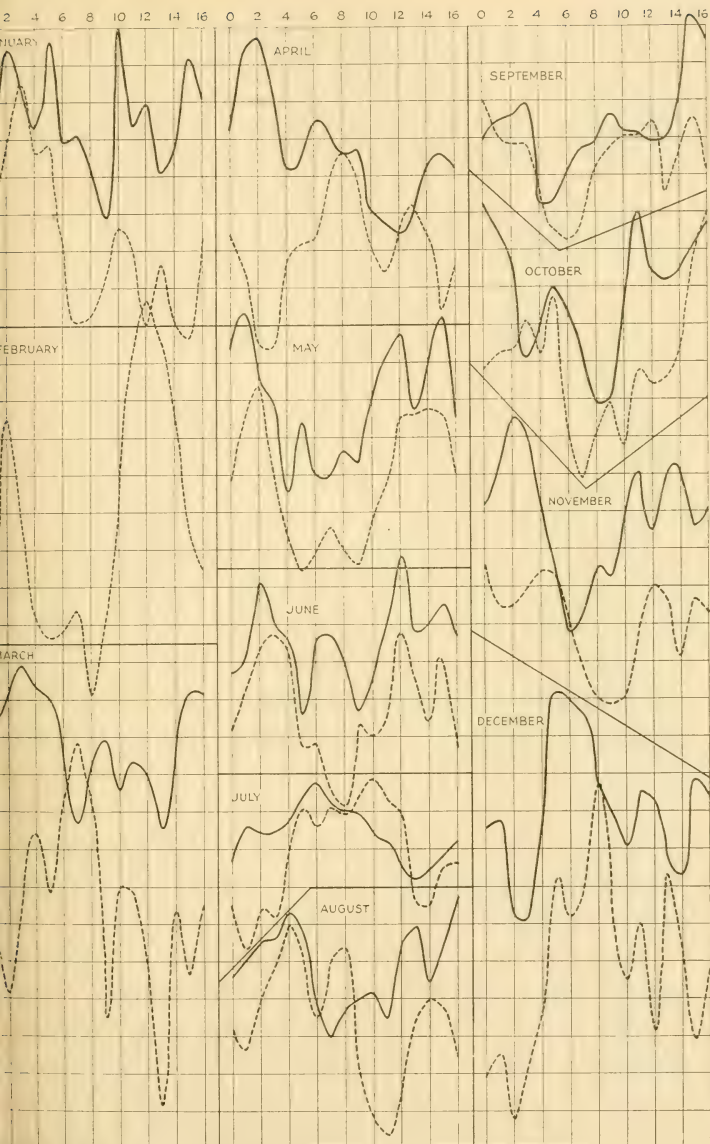
FIG. 3.—Average temperature departures following rising and falling solar variation sequences in April at Washington, 1924 to 1930, compared to selected cases of especially large solar changes. (Several critics having recommended that temperature marches following large and small solar changes should be entirely separately plotted, I have done this for April, 1924 to 1935. The result harmonizes with fig. 3.)



SOLAR VARIATION AND TEMPERATURE  
FIG. 4.—Temperature effects following solar changes

1924 TO 1930  
 1931 TO 1935

# FOR DESCENDING SOLAR CHANGES



DEPARTURES AT WASHINGTON

1924 to 1930 compared to those 1931 to 1935.





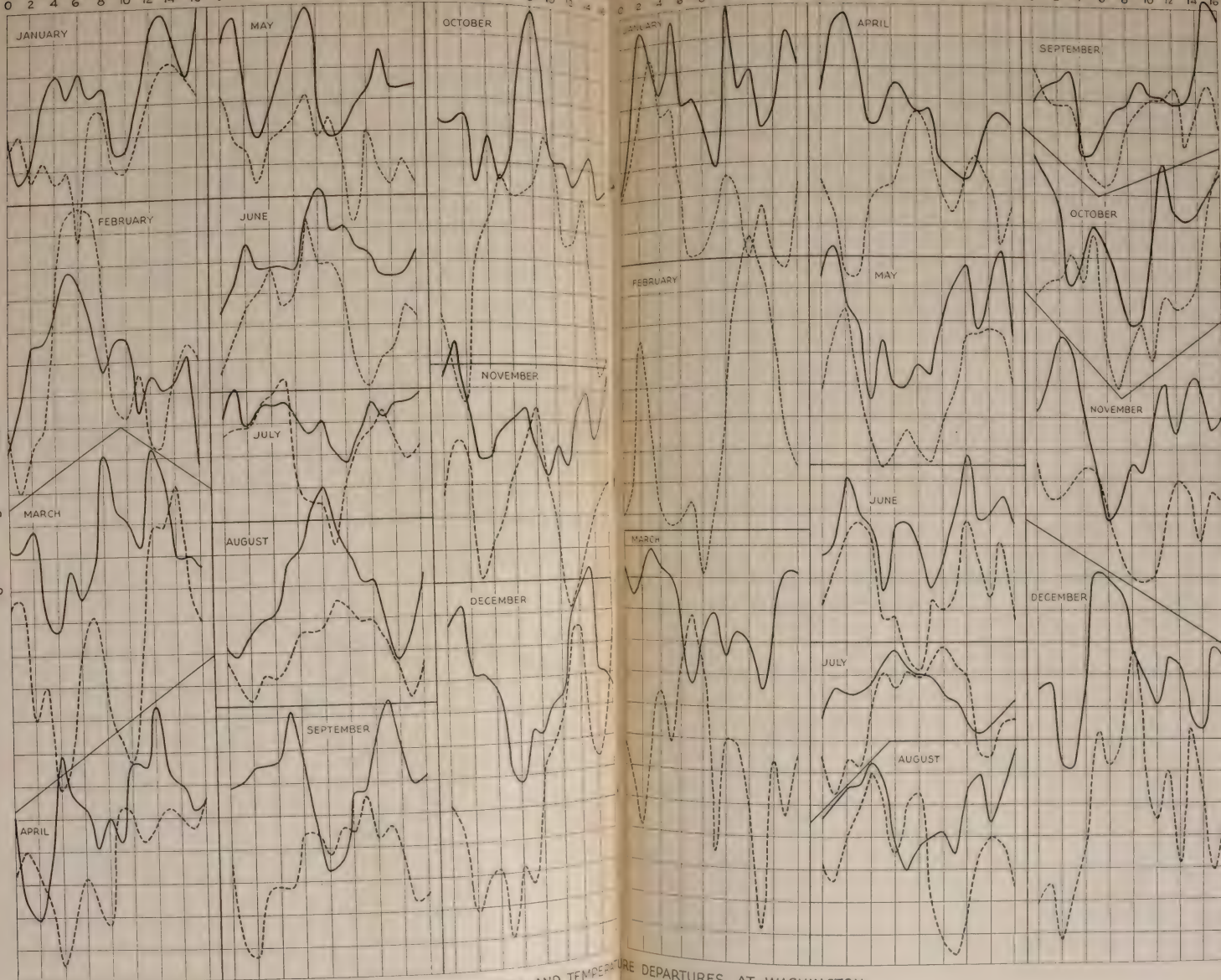
# FOR ASCENDING SOLAR CHANGES

# FOR DESCENDING SOLAR CHANGES

DAYS AFTER START OF SOLAR CHANGE  
0 2 4 6 8 10 12 14 16

FULL CURVES, AVERAGES 1924 TO 1930  
DOTTED CURVES, AVERAGES 1931 TO 1935

TEMPERATURE SCALE FAHR.  
0 5 10



SOLAR VARIATION AND TEMPERATURE DEPARTURES AT WASHINGTON

FIG. 4.—Temperature effects following solar changes 1924 to 1930 compared to those 1931 to 1935.



errors in solar-constant work which, combined, produce still more disturbing distortions in these more meager averages than those occurring in the general mean curves representing more numerous data. On the whole, however, it seems clear that the first half and last half of the data are in fair accord as to the course of temperature departures following sequences of solar change.

Reverting to figure 2, the principal contrasted temperature features corresponding to rising and falling solar sequences are large, and even surprisingly so. In many of the months, temperature changes at Washington exceeding  $5^{\circ}$  Fahrenheit are found in each curve of the pair. In some months, as October, December, and February, the larger ranges even exceed  $10^{\circ}$  Fahrenheit. Thus we have come upon departures from normal temperature which have nearly as large ranges as the largest of those ordinarily to be met with from day to day in the weather. It is easy to conceive, furthermore, that since the apparent effects last for many days, there may have been individual cases when previous or immediately succeeding solar causes would have produced temperature features in unison with those of the mean curves, whereby individual departures produced by solar causes in such cases may have been nearly or quite twice as large as those here shown. In short, if we admit, as seems justified, that these are the temperature effects produced by solar changes, then we must concede that solar changes are a main if not the principal cause of temperature changes in weather. That average changes of temperature ranging sometimes as much as  $10^{\circ}$  Fahrenheit should be thus produced is perhaps difficult to account for in theory, for the average solar changes discussed here cannot much exceed 0.5 percent. But the curves speak for themselves as to the facts.

We may now inquire whether the fourth criterion is fulfilled. Figures 5 and 6 show the general averages for 12 years, 1924 to 1935, for St. Louis, Missouri, and Helena, Montana. The same dates given in table 1 as incipient dates of solar changes were used, of course, for all stations. It will be seen at once that the oppositeness of features that confronted us in figure 2 is also found almost universally in figures 5 and 6. Without actually reproducing here the curves to show it, the reader may also be assured that our criteria numbered 2 and 3 are also fulfilled in the St. Louis and Helena data.

So the observed variations of the sun, hitherto unrecognized in making forecasts, seem to be main causes of temperature changes in weather. Their effects appear to last for at least 2 weeks. Unfortunately, this cannot be immediately tested as a new method of fore-

casting for 14 days in advance. For since the effects last so long, the solar conditions of a previous week as well as those of a present week combine to govern the weather of the week to come. Hence it would be necessary to have highly accurate solar-constant observations for

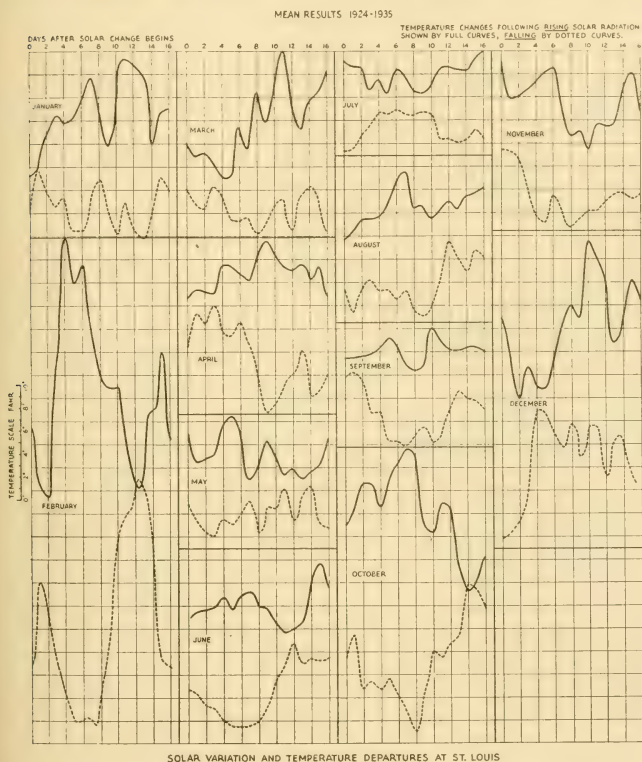


FIG. 5.—Oppositeness of temperature departures at St. Louis which follow average rising and falling sequences of solar variation.

nearly every day in the year in order to attempt to utilize this discovery for weather predictions. Unfortunately, we cannot yet command this information. Three solar-constant stations are indeed in operation, but at least 10 cooperating stations would be required for the purpose.

If means to establish and maintain 10 stations were now available, forecasting by this method could not begin until 1940. For the most

accurate results depend on the use of the "short method." This is empirical, and is based on several hundred solar-constant observations by the "long method" as we now call the fundamental method of Langley. Thus the "establishment" of a station requires several years. If funds were now available, the stations could begin observing

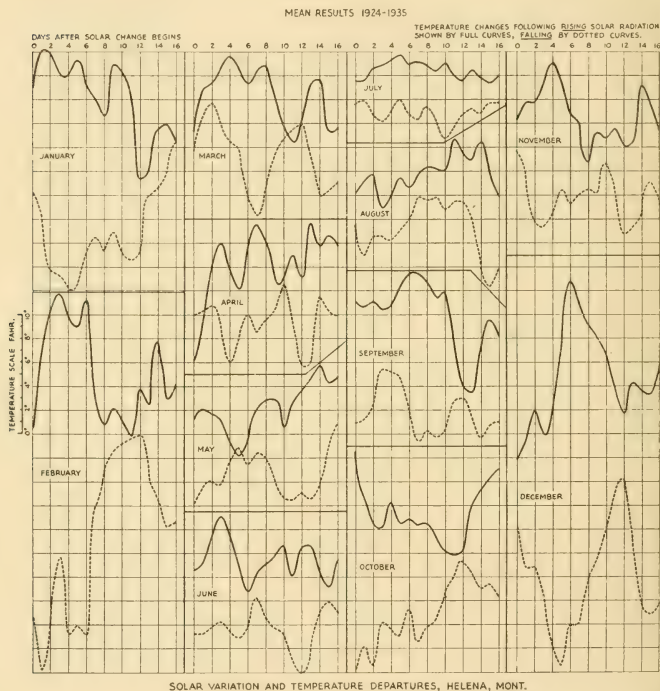


FIG. 6.—Oppositeness of temperature departures at Helena which follow average rising and falling sequences of solar variation.

early in 1938, but the "short method" tables and necessary investigations of weather relationships at many stations would not be completed for forecasting purposes before the end of 1939.

I have thought of another method which may be practicable for following solar changes. As indicated by figure 1, page 29 of volume 5, *Annals of the Smithsonian Astrophysical Observatory*, the

variation of the sun appears to be greater for the shorter wave lengths. It may be even 10 times as great at wave length 3200 angstroms as for the total radiation of all wave lengths combined. Suppose, then, that a silvered hollow ball of Corex glass should be carried by a sounding balloon to 30,000 meters elevation. Every day would be fine there, and a flux of ultraviolet rays for which silver is transparent would flow through the ball, practically as unimpeded by the atmosphere as if actually in free space. If, therefore, by a photoelectric cell, or a photographic record, the intensity of these selected ultraviolet rays could be measured to an accuracy of 1 percent, and quick intelligence of these measurements could reach the home station on the ground, the problem might be solved perhaps better than by multiplying solar-constant observing stations. Yet this new plan has several uncertain features. It would be well if both plans could be tried.

Should an accurate daily series of determinations of solar variation become available, it may well prove that several radically different temperature effects will be discovered for each given station differing with the magnitudes of the solar changes concerned. For it seems reasonable to suppose that until a solar change reaches a certain magnitude local obstacles would impede its effect on temperature. Indeed it must not be expected that the solar variation is a complete guide to weather, but rather a factor in a highly complex problem, the recognition of which may yield valuable progress in weather forecasting.

The reader will note in figures 2, 5, and 6 that the curves differ from month to month and from station to station. As stated by Clayton and others, almost immediate effects of solar changes are found at certain places on the globe which he calls "centers of action." From these the effects spread by atmospheric waves to distant localities. The paths followed by these atmospheric waves doubtless differ with secularly changing meteorological conditions governing atmospheric states in different hemispheres. Hence, doubtless, arise the differences above noted. Note for instance in the month of January that the broadest separation of the pair of curves occurs first at Helena, later at St. Louis, and last at Washington.

It was suggested above that the temperature effects discovered seem at first sight disproportionally large compared to the solar changes which induce them. However, temperatures in the temperate zones depend largely on the prevailing direction of the wind. Clayton has shown that solar changes are accompanied by wanderings of the atmospheric "centers of action." Thence come shiftings of the centers of cyclonic motions of the atmosphere, which, in their turn govern the

direction of the winds at particular localities. Such displacements of the cyclones and anticyclones and wind directions so caused are probably the mechanisms involved in the large effects found in this paper.

#### ADDENDA

#### NOTE ON MR. CLAYTON'S INVESTIGATIONS OF THE RELATIONS OF RADIATION AND TEMPERATURE<sup>1</sup>

By C. G. ABBOT

Nearly 40 years ago the late Secretary Langley, at that time Director of the Allegheny Observatory, made the following remarkable statement in his report of the Mount Whitney Expedition:

"If the observation of the amount of heat the sun sends the earth is among the most important and difficult in astronomical physics it may also be termed the fundamental problem of meteorology, nearly all whose phenomena would become predictable if we knew both the original quantity and kind of this heat; how it affects the constituents of the atmosphere on its passage earthward; how much of it reaches the soil; how through the aid of the atmosphere it maintains the surface temperature of this planet, and how in diminished quantity and altered kind it is finally returned to outer space."

Let us set over against this pronouncement of Langley the final conclusion of Mr. Clayton in the paper which follows: "The results of these researches have led me to believe: 1. That if there were no variation in solar radiation the atmospheric motions would establish a stable system with exchanges of air between equator and pole and between ocean and land, in which the only variations would be daily and annual changes set in operation by the relative motions of the earth and sun. 2. The existing abnormal changes, which we call weather, have their origins chiefly, if not entirely, in the variations of solar radiation."

\* \* \* \*

His whole paper deserves careful attention, but in order to fix in a striking manner in the reader's mind the strength of his case for a real correlation between solar radiation and terrestrial temperature, I would draw attention to tables 1 and 2 of Mr. Clayton's main paper

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<sup>1</sup> Clayton, H. H., Variation in solar radiation and the weather. Smithsonian Misc. Coll., vol. 71, no. 3, 1920.



and to the little table in the Appendix. Part of the data in table 2, changed to the Fahrenheit scale, forms the frontispiece. [Here figure 7.]

\* \* \* \*

I would like to draw the reader's attention in particular to number 7 of the conclusions which Mr. Clayton states in the summary of his research. In this he points out that variations of temperature in Argentina agree well in number and in magnitude to the variations which would be expected in view of the supposed changes in the solar radiation. It is this and many other features of his research which

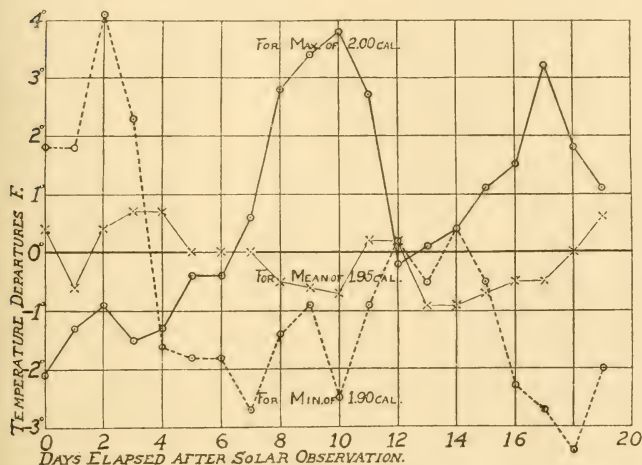


FIG. 7.—H. H. Clayton's indication, published in 1920, of the influence of solar variation on terrestrial temperature departures at Buenos Aires.

have led him to the conclusion that the weather as distinguished from the climate is governed by variations of the sun and would be predictable both qualitatively and quantitatively if we had daily accurate determinations of the solar variation. If this be true, we stand, it seems to me, on the threshold of a very important research in meteorology. What is needed is the establishment of sufficient stations for observing solar radiation, in order that, by combining the results of all of them, well-founded mean solar radiation measurements may be available every day in the year, and for a sufficient succession of years, so that quantitative studies of the dependence of weather conditions on solar variations similar to those of Mr. Clayton may be advantageously pursued.









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# A COMPARATIVE STUDY OF THE LABIUM OF COLEOPTEROUS LARVAE

(WITH EIGHT PLATES)

BY

W. H. ANDERSON

Department of Entomology  
University of Maryland



(PUBLICATION 3393)

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## INTRODUCTION

The study reported on in this paper was undertaken with the idea of comparing the labia of coleopterous larvae and giving the proper connotation to the various parts and plates thereof. The naming of the divisions has been based on a study of muscle origins and insertions. It is hoped that students of systematic entomology may gain some help, either directly or indirectly, from the facts herein reported.

The paper represents the major part of a thesis presented to the faculty of the Graduate School of the University of Maryland in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The author wishes to express his appreciation of the kindness and help of R. E. Snodgrass and Dr. A. G. Böving, of the United States Bureau of Entomology.

## I. GENERAL DISCUSSION OF THE INSECT LABIUM

The labium of insects in its simplest generalized form consists of two major divisions. These parts have been given various names by previous workers, as is shown in the table following, but the most logical system of terminology is that suggested by Snodgrass (1931) because it results from comparative studies of these structures in all

insects and signifies homologous parts through the entire class. For the proximal division of the labium he suggests the term *postmentum*. This division includes the fused cardines of the second maxillae and the part of the labial sternum which is generally accepted as being united with the cardines. The distal division of the labium, that part which always carries the palpi and ligular lobes when these parts are present, is now rather generally known as the *prementum*. It unquestionably represents the *stipites* of the second maxillae.

The main divisions of the labium may remain as single parts, or each may be subdivided into two or more sclerites. Snodgrass (1931, pp. 483-484) states in regard to the *postmentum* that its "sclerotization may take the form of one, two, or even three distinct plates."

The terminology of the labium of insects in general seems somewhat more complicated than the morphology. Perhaps more attention has been given the sclerites than they deserve, considering their secondary significance. The origin of the term *mentum* and its connection with a definite region of the labium is rather obscure, but inasmuch as it means "chin", it was doubtless intended to apply to that part of the fused second maxillae which supports the "lip." Since the word *labium* has a common derivation with "lip", it would seem better, perhaps, to refer to the distal region of the second maxillae, that part which is movable by muscles, as the *labium*. Crampton (1921) has apparently the same idea when he calls the distalmost division of the underlip region the "*eulabium*."

In order to assist in understanding and correlating the systems of terminology for the parts of the labium, the following table has been compiled. It shows the names that have been applied to the same divisions by the indicated workers.

Comstock (1924)	Kadić (1902)	Snodgrass (1928)	Walker (1931)	Modern usage adopted in this paper
Ligula.....	Mentum.....	Mentum....	Mentum....	Prementum
Mentum....	Vorderplatte of submentum	Submentum	Secondary submental plate	Mentum
Submentum.	Submental- platte		Primary submental plate	
				Submentum
				Postmentum

The complete musculature of the labium (salivary pump muscles omitted) based on the condition as found in some of the more generalized forms (roach, pl. 1, B; cricket, Snodgrass, 1931, fig. 24) is shown in the diagrammatic representation (pl. 1, A). It shows the

labium as made up of two main divisions, the prementum (*Prmt*), and the postmentum (*Pmt*). The postmentum is in turn divided by a suture into the mentum (*Mt*) and the submentum (*Smt*). These are the parts in the usual three-part labium, although this seems infrequently to be the case in coleopterous larvae, as will be shown later.

Kadić (1902) showed that the mentum and submentum are to be considered as secondary subdivisions of the basal part of the labium and that therefore the labium is fundamentally made up of two regions. Walker (1931), after a study of the labial muscles, substantiates Kadić's view, namely that the mentum is in reality a sclerite of the basal region. While holding to the same viewpoint as to the importance of the divisions, it has been thought best in this paper to use the terms *mentum* and *submentum* for the two basal subdivisions, and adopt the term *postmentum* for the combined areas as suggested by Snodgrass (1931).

The prementum bears the palpi (pl. 1, A, *Plp*) and the ligula (*Lig*). The latter consists typically of four lobes, a median pair of glossae (*Gl*) and a lateral pair of paraglossae (*Pgl*). The postmentum is subdivided into two divisions, the mentum (*Mt*) and the submentum (*Smt*).

A description of the seven pairs of muscles found in the generalized labium follows:

The depressors of the palpus (pl. 1, A, *dplp*) arise in the prementum near or on the margin of a median slit which in some cases divides the prementum nearly to its base. These muscles insert on the distal margin of the basal segment of the palpus (*Plp*).

Opposing the muscles just described are the levators of the palpus (*lplp*). These also originate in the prementum close to its postero-lateral angles. In some cases (*Periplaneta*, pl. 1, B) these muscles arise from a pair of small separate sclerites which lie close to the base of the prementum. In keeping with their function of opposing the depressors, they insert on the proximal margin of the basal segment of the palpus.

The flexors of the glossae (*fgl*) have their origin ventrally (posteriorly) on the prementum. They insert on the base of the glossae. The flexors of the glossae and those of the paraglossae lie ventral (posterior) to the depressors of the palpi.

The flexors of the paraglossae (*fpgl*) originate also on the prementum and extend more or less parallel to the flexors of the glossae. They insert on the base of the paraglossae.

The dorsal (anterior) adductors of the labium (*ladlb*) arise on the tentorium (*Tent*) close to the point of origin of the ventral adductors,

but as a rule lateral to the latter. They insert on the dorsal (anterior) surface of the prementum near the bases of the paraglossae. In the large majority of cases their points of insertion are distal to those of the ventral adductors.

The ventral (posterior) adductors (*adlb*) usually originate, as stated above, on the tentorium medially to the dorsal adductors. They insert on the base of the prementum, usually on the main sclerite but sometimes (as in *Periplaneta*) on a pair of smaller sclerites (*B, b, b*). This pair of muscles and that described in the preceding paragraph may work together or oppose one another.

The retractors (or flexors) of the prementum (*rst*) are median muscles which originate from the submental subdivision (*A, Smt*) of the postmentum (*Pmt*). They insert on the base of the prementum, and in nearly all cases their points of insertion are posterior to those of any other pair of labial muscles.

From the preceding descriptions it can be seen that the typical labium may be separated into its two major divisions, the prementum and the postmentum, on the basis of the insertions of the dorsal and ventral adductors of the labium, and the retractors of the prementum. It has become well established by previous investigators that the retractors and adductors insert in all cases only on the prementum. That the mentum, a subdivision of the postmentum, contains no muscle insertions is shown by examples: *Periplaneta* (pl. 1, B) and the labium of adult *Harpalus* (pl. 1, C). It is necessary to accept this interpretation if we are to gain the consistency essential to a comprehensive understanding of the labial structure.

In the larvae of Coleoptera the prementum and the postmentum are again the principal regions of the labium. The postmentum is made up of two distinct subdivisions in *Orthosoma* (pl. 7, A) and in *Ptilodactyla* (pl. 6, B), but it may be a single area as in *Byrrhus* (pl. 1, D). The prementum in coleopterous larvae is very often subdivided so that confusion has arisen in giving the proper connotation to the parts. Taking *Byrrhus* as a typical example of this condition, we find the prementum made up of two sclerites or divisions which are here called the first prementum (*IPrmt*) and the second prementum (*IIPrmt*). Neither one of these is to be considered as secondary to the other since both have the same value morphologically. The second prementum, in all species studied, serves as the area on which the retractors of the prementum insert. In general this subdivision has been considered by previous investigators to be the mentum, but the fact that muscles do insert on it shows that it is impossible correctly to call it the mentum in the sense of the term as applied to the

more generalized forms. The term second prementum shows that it is a part of the prementum, to which it belongs.

In order to clear up any confusion that the preceding discussion may have caused, the possibilities of subdivision in the labium of the larvae of Coleoptera, based on the facts as actually observed, are shown in the following table.

Labium.....	{	Prementum.....	{	First prementum	}	.....	Prementum
				Second prementum			
	{	Postmentum.....	{	Postmentum.....	}		{
							Mentum
							Submentum

In the forms studied there was found no example of a labium consisting of four parts, *i. e.*, a first prementum, a second prementum, a mentum, and a submentum. In no case did a true mentum occur together with a second prementum. The first prementum corresponds to the prementum of previous students of these larvae. It carries the palpi, and in nearly all forms the ventral adductors of the labium are inserted on its base.

In the drawings of the labia, representing the various families, the ventral muscles only have been shown, with a few exceptions. These, the ventral adductors of the labium, and the retractors of the prementum (when present) definitely determine the morphological relationships of the divisions of the labium and serve as criteria for defining them.

The gular region in the larvae of Coleoptera has been the subject of considerable difference of opinion as to its definite boundaries. Crampton (1921) shows that in certain insects (termites and others) the gula and submentum are fused into a single "gularmental plate", and that the posterior portion of this sclerite, fused with the head, is the gula. The conspicuous elongation of this region in certain coleopterous larvae (as for example Tenebrionidae, pl. 5, C) has been shown by Snodgrass to be an adaptation for preserving the vertical plane of the foramen magnum in the development of the prognathous type of head.

The gula is defined by Böving and Craighead (1932) as the "area behind submentum, separated from this by a real or imaginary suture between posterior articulations of the two cardines." Since, however, there are numerous cases (Meloidae, pl. 7, C) in which the retractor muscles of the prementum originate on the anterior portion of this area, that part from which these muscles arise should be considered as at least making up a part of the postmentum. For this reason it is preferable to consider the gula as the area between the anteriorly extended lower ends of the postoccipital suture lying behind a line drawn between the posterior tentorial pits.



## COMPARISON OF THE VARIOUS TYPES OF LABIAL STRUCTURE

As has been previously stated, the labium of insects in its primitive state (pl. 1, A) is made up of two major divisions, the prementum (*Prmt*) lying distal to the insertions of all labial muscles, and the postmentum (*Pmt*) lying proximal to the insertions of all labial muscles.

The roach, *Periplaneta* (pl. 1, B), conforms to this scheme, although the ventral adductors of the labium (*∞adlb*) insert on small lateral sclerites (*b, b*). These are, however, unquestionably but secondary subdivisions of the prementum (*Prmt*). The submental (*Smt*) division of the postmentum (*Pmt*), which is made up in the roach and the adult Coleoptera (*C*) of the submentum and the mentum (*Mt*), serves as the area from which the retractors of the prementum (*B, rst*) originate. The ventral adductors of the labium (*∞adlb*) arise in the typical arrangement from the tentorium.

In adult Coleoptera, of which *Harpalus* (*C*) serves us as an example, the muscles again correspond to the primitive condition. The retractors of the prementum (*rst*) arise from a short and low internal ridge, which is common to the two components of the muscle. This ridge is marked externally by a slender band of extra heavy sclerotization lying in the submentum (*Smt*). The ventral adductors (*∞adlb*) again arise from the tentorium, but their point of origin is nearly contiguous with the submentum, being in the angle formed internally between the latter and the tentorial arms. These muscles insert on the prementum at the posterior margins of the segmentlike bases of the palpi (*Plp*).

As a typical example of the labium of coleopterous larvae, *Byrrhus* was chosen (pl. 1, D). "Typical" is used here in the sense that the conditions of muscular arrangement and labial division, as shown in *Byrrhus*, represent those found in the majority of the larvae studied. That is, more larvae conform to this arrangement than to any other.

The prementum of *Byrrhus* is made up of two divisions, the first and second prementum (*D, IPrmt, IIPrmt*). The postmentum (*Pmt*), however, is not subdivided and consists of a single sclerite. Either the mentum, as found in the generalized forms and in some larvae, has been lost or is inseparably fused with the submental sclerite to form the postmentum.

On the base of the second prementum are inserted the retractors of the prementum (*rst*), which, in common with the generalized condition, arise from the postmentum. The ventral adductors of the labium (*∞adlb*) insert on the base of the first prementum, close to the midventral margin of the latter. They likewise conform with the primitive labium in having their origin on the tentorium (*Tent*).

The dorsal adductors (*radlb*) are typical in so far as their insertion is concerned, since they attach on the first prementum. Their point of origin, however, shows considerable divergence, since they arise, not from the tentorial bar but from the internal surface of the postmentum, near the point of origin of the retractors of the prementum.

That *Byrrhus* is not alone in having muscles other than the retractors of the prementum arising from the postmentum is shown by several outstanding examples, among which are *Pytho* sp. (pl. 5, D), *Lagriidae* (pl. 5, F), *Cucujus clavipes* (pl. 3, F), and *Languria laeta* (pl. 3, E). Such findings are in direct contradiction to the statement of Snodgrass (1935, p. 149), and to make the facts agree we must consider that the origins of muscles may migrate to a certain degree. It is to be noted, however, that except in very unusual cases of migration (*Chauliognathus*, pl. 6, C) the muscular origins have not moved very far. In most cases when the point of origin is on the postmentum, it is directly ventral to the tentorial bar which extends across the head between the tentorial pits, as shown in *Byrrhus* (pl. 1, D).

## II. DESCRIPTIONS OF LABIA OF COLEOPTEROUS LARVAE

*Cicindelidae*<sup>1</sup> (pl. 2, A, B).

The labium of *Cicindela* sp. is made up of a rather compact and firmly united prementum (A, *Prmt*) attached to the head capsule by a membranous area, which, as in other representatives of the Adephaga, is called the mentum (*Mt*). The submentum (*Smt*), if it should be considered as being present, has lost what membranous connection it may have had with the head capsule and is inseparably united with the ventral wall of the head.

At the base of each palpus (*Plp*) in the species studied there is a small sclerotic area divided by a suture, which acts as a hinge. This sclerite is in very close union with the palpus and also with the basal sclerite of the prementum, which partially surrounds it at the base and extends forward, as a bar, beyond the bases of the palpi. The latter sclerite stops at the margin of the head capsule to which it is connected by the membranous mentum, but the above-mentioned bar extends posteriorly into the head for some distance. Thus we must consider the bar as a continuation of the basal sclerite of the prementum.

Two bundles of muscle fibers (A, B, *lplp*), one on either side, arise from this bar, within the head capsule. They insert on the

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<sup>1</sup>The families of Coleoptera have been arranged in the systematic order of Böving and Craighead (1930, pp. 70-80).

sclerite at the base of the palpus, their points of insertion being indicated by the black spot on each sclerite just posterior to the hinge or suture previously mentioned.

No other muscles within the labium may be found, and with the palpi as well developed as they are, it is apparent that these are levators of the palpus. At least this is certainly their functional significance.

Inserted on the inner end of the barlike structure above described is a pair of muscles (A, B, *2adlb*). These muscles originate from the tentorium, but not from its base near the posterior tentorial pits. Instead the origins have migrated dorsally along the posterior arms and even onto the anterior arms (B, *AT*). That they do originate from the anterior arms, in part at least, is shown by the fact that the dorsal arms (*DT*) of the tentorium which arise as secondary outgrowths of the anterior arms, are given off ventral to the attachment of the dorsalmost fiber of this labial muscle. That the dorsal arm is present is proven by the fact that the antennal muscles (*MAnt*) arise therefrom.

Apparently, therefore, the labium consists entirely of a prementum with its appended parts, connected with the head by a membranous mentum. The sclerite of the basal segment of the palpus has become secondarily broken up. Whether or not the submentum is present is difficult to state since from what is considered this region in closely related forms (see below), there arise the adductors of the maxillary stipes (A, *adst*), although a portion of this muscle originates also from the posterior tentorial arm close to the posterior tentorial pit (*pt*).

When the ventral adductors of the labium contract they cause the prementum to tip outward from the head, or ventrally, with the fulcrum of the lever at the margin of the head capsule.

*Carabidae* (pl. 2, C).

The labium of *Harpalus* sp. is separated into a well-marked prementum (*Prmt*), a membranous mentum (*Mt*), and a much narrowed submentum (*Smt*) and gula (*gu*). The posterior tentorial pits (*pt*) lie close together, just lateral to the sutures which mark off this narrowed area.

The ventral muscles of the labium consist of only one pair, the ventral adductors of the labium (*2adlb*). They arise on the arms of the posterior tentorium (*Tent*) and insert at the base of the prementum. Since the sclerotization of the mentum is lacking, these muscles serve to retract the prementum.

*Dytiscidae* (pl. 2, E).

The labium of *Dytiscus* sp., as in other representatives of the Adephaga, has the prementum (*Prmt*) and the mental (*Mt*) subdivision of the postmentum distinguishable from the head capsule. The remainder of the postmentum, *i. e.*, the submentum (*Smt*), has become immovably united with the head. The prementum bears the palpi. The mentum is short and does not show in a live specimen when the prementum is retracted. Korschelt (1924) states, in regard to *Dytiscus marginalis*, that, "Das Mentum is rudimentär. Das Submentum fehlt ganz, und ebenso ist die Ligula vollständig rückgebildet." The submentum (*Smt*) as a separate sclerite has disappeared, but it is interpreted as lying anterior to the tentorial pits (*pt*).

The muscles inserting on the prementum consist of two pairs of adductor muscles. The ventral adductors (*2adlb*) originate on the tentorium, at or close to the point of invagination of the latter, and insert on the base of the prementum. Their points of insertion are closer to the midline than is the case in many larvae. The dorsal adductors of the labium (*1adlb*) originate also on the tentorium but, contrary to their custom, they insert ventrally on the base of the prementum. Proof that these are really the migrated dorsal adductors lies in the fact that their point of origin is, as usual, ventral to that of the ventral adductors. Furthermore, the point of insertion of the ventral adductors has migrated perceptibly toward the midline of the base of the prementum, allowing room for the dorsal adductors.

*Gyrinidae* (pl. 2, F).

In *Dineutes* the two parts of the labium that are present and separate from the head capsule are the mentum (*Mt*) and a split prementum (*Prmt*). The submentum (*Smt*) has become completely fused with the skeleton of the head and is not distinguished from the latter by any indication of a suture. The prementum in *Dineutes* is unique among the larvae studied in that it is very deeply furcate in the midline. The two parts have the appearance of basal segments of a three-segmented palpus, but their musculature proves them to be halves of a cleft prementum. The mentum (*Mt*) is better developed than it was in the larvae previously discussed.

The muscles of the labium are the two pairs of adductor muscles which usually insert on the prementum. The ventral adductors (*2adlb*) originate on the submentum, apparently having migrated there from their more primitive position on the tentorial arms. They insert on the bases of the halves of the prementum, and to judge from their position, no doubt act as depressors of the palpuslike structure, which is made up of a palpus (*Plp*) and one-half the prementum (*Prmt*).

The dorsal adductors (*iadlb*) have their origins on the tentorial invaginations and insert on the bases of the divided prementum. Fulfilling their usual rôle of opposing the ventral adductors, they apparently act as levators of the combined palpus and half prementum.

*Silphidae* (pl. 3, A).

The labium of the larva of *Silpha* shows for the first time, in our study of the labia by families, a three-part labium, all components of which are distinctly separated from the head. As in *Byrrhus* (pl. 1, D), the first prementum (pl. 3, A, *IPrmt*), the second prementum (*IIPrmt*), and the postmentum (*Pmt*) cooperate in the formation of the three-part labium. They are set off from one another by distinct membranous areas. Furthermore, the postmentum is definitely separated by a suture from an incipient gula (*Gu*).

*Silpha* differs from *Byrrhus* in that the ventral adductors of the labium (*adlb*) arise on the postmentum rather than on the tentorium (pl. 1, D). In the form studied the tentorial pits (pl. 3, A, *pt*) lie very closely approximated and immediately behind the base of the postmentum. Apparently the ventral adductor muscles have moved their points of origin from the tentorial arms to the base of the postmentum. Up to this point in our consideration of the labium of the various families no retractor muscles of the prementum have been observed. In *Silpha* however these muscles (*rst*) are present. They originate from the postmentum and insert on the base of the second prementum.

*Staphylinidae* (pl. 3, B).

The labium of *Hesperus* appears to consist of only two parts which are distinct from the head. The submentum (*Smt*) is again combined with the head capsule, as in the representatives of the Adephaga. It differs from them however in having the submentum definitely marked off laterally by sutures or grooves. The prementum (*Prmt*) bears the palpi and a simple ligula. The mentum (*Mt*) is membranous almost throughout but has a narrow sclerite at its base.

There is present only one pair of ventral muscles. These, the ventral adductors of the labium (*adlb*), originate on the bases of the tentorial arms and insert on the base of the prementum.

*Histeridae* (pl. 3, C).

In *Hololepta* the labium is similar to several of the preceding in that it consists of a clearly marked prementum (*Prmt*) set off from the head capsule by a membranous mentum (*Mt*). Also the submentum (*Smt*) is completely fused with the head capsule although



demarcated by definite lateral grooves or sutures. The gula is narrowed to the extent that the sutures which usually bound it laterally have fused completely, forming a so-called gular suture (*gs*).

There is only one pair of ventral muscles to be found in the labium of this insect. These, the ventral adductors of the labium (*zadlb*), originate from the posterior tentorium. They insert on the base of the prementum.

*Hydrophilidae* (pl. 3, D).

The postmentum (*Pmt*), the second prementum (*IIPrmt*), and the first prementum (*IPrmt*) cooperate in the formation of the labium of *Hydrous*. The first prementum bears the palpi and the ligula (*Lig*). The latter is smaller than in most members of this family, but it is nevertheless clearly differentiated. The second prementum is broad, and its lateral anterior margins are greatly extended. In this respect it resembles the mentum of many adult beetles (pl. 1, C). It is separated by a well-defined membranous area from the postmentum. About midway of the lateroposterior margins of the latter are found the tentorial pits (*pt*).

From the condition of the labium as above mentioned it would be expected that there are two ventral pairs of muscles, the ventral adductors of the labium (pl. 3, D, *zadlb*) and the retractors of the prementum (*rst*). The adductor muscles originate from the tentorial arms near their bases, the posterior tentorial pits (*pt*). They converge somewhat and insert on the base of the first prementum. The retractor muscles consist of a single broad bundle in place of the more usual two strands. They originate from nearly the complete posterior width of the postmentum and insert along the base of the second prementum.

*Languriidae* (pl. 3, E).

The labium of *Languria* is divided into three distinct divisions, the first prementum (*IPrmt*), the second prementum (*IIPrmt*), and the postmentum (*Pmt*). Posterior to the base of the distal division is the gula (*Gu*). The parts of the labium are separated by distinct sutures but not by areas of membrane as in some forms.

There are two pairs of ventral muscles which serve as criteria for properly naming the constituents of this labium. The shorter of these, the retractors of the prementum (*rst*), arise from the postmentum and insert on the base of the second prementum. The second pair, the ventral adductors of the labium (*zadlb*), as in *Byrrhus*, originate from the postmentum and not from the tentorium. They insert on the base of the first prementum.



*Silvanidae* (pl. 3, G).

The customary division of the labium into a first prementum (*IPrmt*), a second prementum (*IIPrmt*) and a postmentum (*Pmt*) is found in *Oryzaephilus*. The first prementum carries the palpi and one pair of setae. The second prementum also bears a pair of setae situated just before the middle. The postmentum is shorter than the second prementum and at its posterolateral margins are located the posterior tentorial pits (*pt*). On the postmentum also are found two setae, near its anterior boundary.

The ventral muscles consist of two pairs, the ventral adductors of the labium (*adlb*) and the retractors of the prementum (*rst*). The latter have their origin on the postmentum in the region of the tentorial pits and insert on the base of the second prementum. The adductor muscles also arise from the inner surface of the postmental sclerite, medial to the retractor muscles. They insert on the base of the first prementum.

*Cucujidae* (pl. 3, F).

The labium of *Cucujus* shows the usual three subdivisions. The distal part, which bears the palpi and is separated from the proximal parts by a distinct membranous area, is the first prementum (*IPrmt*). The second prementum (*IIPrmt*) is separated from the postmentum by a second membranous area. The postmentum (*Pmt*) and the gula (*Gu*) are fused into one sclerite with no dividing suture. This sclerotized area is bounded laterally by the posterior tentorial pits (*pt*) and the postoccipital suture (*pos*), and posteriorly by the margin of the foramen. The gula is interpreted as that portion of this sclerite which lies posterior to an imaginary line connecting the posterior tentorial pits.

The ventral adductors of the labium (*adlb*), as in *Byrrhus*, arise from the postmentum instead of from the tentorium. These points of origin, however, are on a line with the posterior tentorial pits, and it is apparent that they have migrated from the tentorial bridge to their present location. Their points of insertion, on the base of the first prementum, are consistent. The retractors of the prementum (*rst*) arise from the customary place on the postmentum, slightly anterior to a line connecting the tentorial pits.

*Laemophloeidae* (pl. 3, H).

In *Eunausibius* the labium is separated into three regions, the first and second subdivisions of the prementum, and the postmentum. The first prementum (*IPrmt*) bears the palpi. The second prementum (*IIPrmt*) is marked off anteriorly and posteriorly by distinct sutures. The latter area bears a pair of setae which are situated slightly before

the middle, and a smaller pair located near the posterolateral margins. The postmentum (*Pmt*) is marked laterally by the posterior tentorial pits (*pt*) and posteriorly by the ventral margin of the foramen.

The ventral adductors of the labium (*adlb*) arise on the cross bar or bridge of the tentorium and insert on the base of the first prementum. The retractors of the prementum (*rst*) arise on the proximal part of the postmental area and insert on the base of the second prementum.

*Nitidulidae* (pl. 4, A).

The labium of this family is made up of three divisions, only one of which belongs to the prementum. The posterior two parts are subdivisions of the postmentum. The prementum (*Prmt*) bears one pair of setae which arise from the rather distinctly shaped sclerite of the prementum. It also carries the palpi which consist of only one segment in contrast to the usual condition of two segments. The mentum (*Mt*) is separated from the preceding division by a comparatively broad membranous area. It bears one pair of large setae. In the species figured the mentum and submentum (*Smt*) are separated by a weakly indicated groove, but in other species of the family the separation is very clearly marked (Böving and Craighead, 1930, pl. 35, fig. B). The submentum has a rather peculiar urn shape and extends to the posterior margin of the head.

There is only one pair of ventral muscles in the labium. The lateral elements of this muscle, the ventral adductors of the labium (*adlb*), at their point of origin, unite in the midline of the submentum and diverge slightly to their insertion on the sclerite at the base of the prementum.

*Endomychidae* (pl. 4, B).

The labium of *Endomychidae* shows two divisions, the prementum (*Prmt*) and the postmentum (*Pmt*). The prementum bears the palpi and a short ligula. It also has on its ventral surface a pair of setae which are situated slightly proximal to the bases of the palpi. The postmentum (*Pmt*) extends posteriorly to the neck membrane and makes up the larger portion of the labium. On it are located two pairs of setae and an unpaired median seta near the distal margin. Bounding the postmentum on its posterolateral margins are the posterior tentorial pits (*pt*).

The ventral muscles, as would be expected, are only one pair, the ventral adductors of the labium (*adlb*). They originate on the tentorium (*Tent*) and proceed obliquely from their points of origin to insert on the base of the prementum, where they nearly meet in the midline.

*Dacnidae* (pl. 4, D).

The representative of this family, *Tritoma unicolor* Say, agrees with the general type in having a three-part labium made up of the first prementum (*IPrmt*), the second prementum (*IIPrmt*) and the postmentum (*Pmt*). The first prementum carries the palpi and one pair of setae. It is separated from the second prementum by a suture. The postmentum is somewhat unusual in that its lateral margins are extended anteriorly to the level of the base of the first prementum. The posterior margin of the postmentum is marked by a definite suture, separating it from the gula (*Gu*).

The ventral adductors of the labium (*zadlb*) originate on the posterior arms of the tentorium, close to the tentorial pits (*pt*). They insert on the base of the first prementum. The retractors of the prementum (*rst*) originate at or very near the tentorial pits. Their point of origin so closely approaches the tentorium that it is impossible to state definitely whence they arise. It is thought that they originate in the angle between the tentorial arms and the postmentum. They insert on the base of the second prementum.

*Anthicidae* (pl. 4, E).

*Anthicus* has a labium which shows the usual three divisions of first prementum (*IPrmt*), second prementum (*IIPrmt*), and postmentum (*Pmt*). In addition there is present a distinct gula (*Gu*) separated from the postmentum by a definite suture. Each division of the labium is set off from the others by sutures or grooves.

There are two pairs of ventral muscles, the retractors of the prementum (*rst*) and the ventral adductors of the labium (*zadlb*). They have the generalized origins and insertions. The adductor muscles arise on the tentorium (*Tent*) and insert on the base of the first prementum. The retractors have their origin on the postmentum, just anterior to the posterior margin of the latter, and insert on the base of the second prementum.

*Byturidae* (pl. 4, F).

The labium of *Byturus* is like that of the preceding family in that it consists of three divisions, the postmentum (*Pmt*), the second prementum (*IIPrmt*), and the first prementum (*IPrmt*). Behind the postmentum and marked laterally by the posterior tentorial pits (*pt*) is the gula (*Gu*).

There are two pairs of ventral muscles in this species. The retractors of the prementum (*rst*) originate from the posterior margin of the postmentum and insert on the base of the second prementum.

The ventral adductors of the labium (*zadlb*) arise from the tentorial bridge (*Tent*) and insert at the base of the first prementum.

*Colydiidae* (pl. 4, G).

The labium of the representative of the family Colydiidae shows no departure from the customary structure of this group. The usual three divisions are clearly marked and readily interpreted from a study of the musculature. The first prementum (*IPrmt*) bears the palpi and in addition two pairs of setae, the proximal pair much shorter than the distal pair. The second prementum (*IIPrmt*) likewise carries two pairs of setae. It is separated by membranous areas from the first prementum distally, and from the postmentum (*Pmt*) proximally. The latter bears, near its anterior margin, two pairs of setae, the distal pair of which is exceptionally long and slender. The lateroposterior margins are marked by the posterior tentorial pits (*pt*).

There are two pairs of ventral labial muscles, neither of which presents any unusual features. The ventral adductors of the labium (*zadlb*) originate from the tentorial bridge (*Tent*) and insert on the base of the first prementum. The retractors of the prementum (*rst*) arise from the posterior region of the postmentum and insert on the base of the second prementum.

*Mycetophagidae* (pl. 4, C).

The prementum of *Mycetophagus* is subdivided into the first prementum (*IPrmt*) and the second prementum (*IIPrmt*). Each of these divisions bears one pair of setae and is separated from the other by a membranous area. The second prementum is set off from the postmentum (*Pmt*) by a second area of membrane. The postmentum has one pair of setae, located slightly before and mesal to the anterior ends of the tentorial pits (*pt*). There is a slight indication of a groove or suture (indicated in the figure by a broken line) which connects the anterior ends of the tentorial pits. This may be a rudiment of a previously well-marked boundary line between the postmentum and the gula (*Gu*). This is quite possible because of the fact that the retractors of the prementum originate on the postmentum just anterior to this line.

The ventral adductors of the labium (*zadlb*) have their origin on the tentorium (*Tent*) and insert on the base of the first prementum. The retractors of the prementum (*rst*) arise from the posterolateral portion of the postmentum and insert on the base of the second prementum.

*Synchroidae* (pl. 5, A).

The first prementum (*IPrmt*), which is clearly set off from the second prementum by membrane, bears a pair of setae situated just

behind the bases of the palpi. The ligula is rather more enlarged than ordinarily, and it has a considerable group of sensory setae distributed on its distal portion. The second prementum (*IIPrmt*) has two pairs of setae located close to the lateral margins about midway from the distal to the proximal boundary. The postmentum (*Pmt*) is separated anteriorly from the prementum by a suture and is interpreted as extending to the posterior margin of the head. The proximal portion of the postmentum lies between the tentorial pits (*pt*) and probably includes an undifferentiated gular region.

The ventral muscles have the customary origins and insertions. The ventral adductors of the labium (*zadlb*) arise on the tentorium (*Tent*) and insert on the base of the first prementum near the midline. The sclerite of the first prementum has become extended slightly posteriorly in the center to form a point of attachment for these muscles. The retractors of the prementum (*rst*), a comparatively large pair of muscles, arise on the postmentum and insert on the base of the second prementum.

*Pyrochroidae* (pl. 5, B).

The customary division of the labium into the first prementum and the second prementum, together with the postmentum, is shown by this species. The labium is somewhat unusual in that it has a considerably elongated ligula (*Lig*). The postmentum (*Pmt*) is separated from the second prementum (*IIPrmt*) by a membranous area, and extends posteriorly as far as the proximal ends of the posterior tentorial pits (*pt*). The gula (*Gu*) is a separate sclerite lying posterior to the tentorial pits and the postmentum.

There are the usual muscles in this species. The retractors of the prementum (*rst*) arise on the postmentum in line with the anterior ends of the tentorial pits and insert on the base of the second prementum. The ventral adductors of the labium (*zadlb*) originate from the posterior tentorium (*Tent*) and insert on the base of the first prementum (*IPrmt*).

*Pythidae* (pl. 5, D).

In external appearance the labium of *Pytho* shows no unusual features, although it does carry a prominent ligula (*Lig*). The first prementum (*IPrmt*) carries the palpi and is set off from the second prementum (*IIPrmt*) by a membrane. The postmentum (*Pmt*) is likewise separated from the latter subdivision by a membranous area.

There are two pairs of ventral muscles to be found in the labium of this species. The retractors of the prementum (*rst*) originate on the postmentum and insert on the base of the second prementum.



Their points of insertion are noticeable from the exterior as small ovals more heavily sclerotized than the surrounding integument. The ventral adductors of the labium (*adlb*) arise from the postmental sclerite and insert on the base of the first prementum.

*Alleculidae* (pl. 5, E).

The first and the second prementum, in this labium, are clearly marked off from each other by a membranous area. The second prementum (*IIPrmt*) is likewise set off from the postmentum (*Pmt*) by a membrane. The postmentum has as its posterior limit an imaginary line connecting the posterior tentorial pits (*pt*). Behind the postmentum, but in no way marked off from it, is the gula (*Gu*). The latter is bounded along the sides by faint indications of the postoccipital suture.

The ventral muscles again consist of two pairs. The ventral adductors of the labium (*adlb*) originate on the tentorium (*Tent*) and insert on the first prementum (*IPrmt*). The retractors of the prementum (*rst*) arise on the postmentum slightly anterior to the tentorial pits and insert on the base of the second prementum.

*Tenebrionidae* (pl. 5, C).

The divisions of the labium of *Merinus* are consistent with the basic scheme of the three-part labium of coleopterous larvae. The gula is definitely separated from the postmentum (*Pmt*) by a suture. It is marked laterally by the posterior tentorial pits (*pt*) and the postoccipital suture (*pos*) and posteriorly by the ventral margin of the postoccipital ridge (*PoR*).

The ventral adductors of the labium (*adlb*) originate on the tentorial arms (*Tent*) and insert on the base of the first prementum. The usually paired retractors of the prementum (*rst*) are united in this species into a comparatively large median bundle which arises from the posterior margin of the postmentum. It inserts on the base of the second prementum.

*Lagriidae* (pl. 5, F).

There are seen in the representative of this family the usual three divisions of the labium, the postmentum (*Pmt*), the second prementum (*IIPrmt*), and the first prementum (*IPrmt*). The first prementum carries the palpi and a distinct ligula. The second prementum is separated from the preceding subdivision by a membranous strip. The postmentum, lying behind the second prementum, is separated from the latter by a distinct membranous area. The lateral margins of the postmentum diverge toward the proximal margin.



The ventral muscles consist of two pairs, the retractors of the prementum (*rst*) and the ventral adductors of the labium (*zadlb*). The retractor muscles, as is their custom, originate from the postmental sclerite and insert on the base of the second prementum. The ventral adductors also arise on the postmentum, instead of on the tentorium. Their point of origin is almost directly posterior to that of the retractor muscles. As is the usual condition, they insert on the base of the first prementum.

*Byrrhidae* (pl. 5, G).

Since this family shows a type of labium which might be considered generalized for coleopterous larvae, it was adopted as a basic example (pl. 1, D). It shows the three divisions of the labium definitely, the first prementum (pl. 5, G, *IPrmt*), the second prementum (*IIPrmt*), and the postmentum (*Pmt*). The two segmented palpi, conforming to the general condition, are borne on the first prementum. The latter is marked off from the second prementum by a membranous ring, and the second prementum is separated from the postmentum in a similar manner.

Inserted on the base of the first prementum are found the ventral adductors of the labium (*zadlb*). They originate on the cross bar of the tentorium (*Tent*). The retractors of the prementum (*rst*) insert on the base of the second prementum, with their origin on the postmental sclerite.

*Helodidae* (pl. 5, H).

The labium of *Prionocyphon* consists of but two well-marked divisions. Most of the labium is made up of a large prementum (*Prmt*), which bears several pairs of scattered setae. From its anterior margin arise the palpi, which are rather small in comparison with other larvae. Between the prementum and the posteroventral margin of the head capsule is the postmentum (*Pmt*). At its posterolateral margins are the posterior tentorial pits (*pt*).

There are two pairs of ventral muscles, both of which insert on the prementum. The retractors of the prementum (*rst*) originate from the tentorial arms and go diagonally to the base of the prementum where they insert close together in the midline. The ventral adductors of the labium (*zadlb*) are also present. They originate, however, from the postmentum. Their point of insertion is slightly anterior of the center of the premental sclerite. Thus in this insect the origins of the two pairs of ventral muscles are reversed from the more primitive condition as found in the roach (pl. 1, B).

*Nosodendridae* (pl. 6, A).

The labium of *Nosodendron* consists of three clearly marked divisions. From a study of the musculature it is seen that these are the postmentum (*Pmt*), the second prementum (*IIPrmt*), and the first prementum (*IPrmt*). The first prementum carries the palpi and is divided by a distinct groove almost to its base, where the groove joins the apex of a definite triangular piece. The second prementum is marked distally by a membranous band which separates it from the first prementum. It bears near its lateral margins, slightly behind the middle, obliquely directed comblike tufts of hairs. The postmentum lies behind the parts described above. It is nearly square, and at its posterolateral margins are found the tentorial pits (*pt*).

The ventral muscles in the labium consist of the usual two pairs, the ventral adductors of the labium (*zadlb*) and the retractors of the prementum (*rst*). The latter originate from the postmental sclerite, approximately on a level with the internal tentorial bridge (*Tent*). They insert on the base of the second prementum. The ventral adductors arise on the tentorial bar and, proceeding to their insertion at the base of the first prementum, converge and nearly meet in the midline at their point of attachment on the small triangular area previously mentioned.

*Ptilodactylidae* (pl. 6, B).

In the labium of *Ptilodactyla* are found the prementum (*Prmt*), a median mentum (*Mt*), and a proximal submentum (*Smt*). The two latter parts together form the postmentum. The prementum bears the palpi and a prominent ligula (*Lig*). The mentum, separated from the prementum by a membranous area, is considerably broader than the distal division. It is separated from the submentum by a distinct suture and hinge. The latter division is firmly united with the head, although it is set off from it by a suture. In connection with this union it is interesting to note that the posterior tentorial pits (*pt*) have invaded the submentum. The lateral elements of the postoccipital suture have become united into a median suture (*gs*) and unite with the ends of the posterior tentorial pits.

Although the tentorial invaginations are located in an unusual position, it is definitely assured that this posterior division is the submentum because from it originate the ventral adductors of the labium (*zadlb*). They insert on the base of the prementum.

*Cantharidae* (pl. 6, C).

The labium of *Chauliognathus* shows only two parts, the terminal prementum (*Prmt*) and a median oval sclerite surrounded by mem-

brane, the postmentum (*Pmt*). All signs of a gula have become obliterated. The posterior tentorial pits (*pt*), which at their posterior ends are firmly united with the head capsule, extend into the membranous area at the base of the labium.

There are two pairs of ventral muscles, both of which insert on the base of the prementum. The first pair, the retractors of the prementum (*rst*), originate near the posterior margin of the postmental sclerite (*Pmt*). They lie ventral to the second pair, the ventral adductors of the labium (*2adlb*) which arise on the postoccipital ridge (*PoR*). These latter muscles are long and slender, and their points of origin have apparently migrated to their present location, possibly in connection with the loss of the gular region.

*Cebriionidae* (pl. 6, D).

A study of the labium of *Cebrio* shows it to consist of three parts, a prementum (*Prmt*), a mentum (*Mt*), and a submentum (*Smt*). The prementum bears the palpi, and close behind the bases of these are found three pairs of setae, the ones on either side arranged in a straight line. The mentum is an elongate oval sclerite taking up the central region of the labium. The submentum consists of two small, triangular sclerites. They are separate from one another and located near the posterior margin of the labium.

The ventral muscles are only one pair, the ventral adductors of the labium (*2adlb*). They arise from the triangular submental plates and insert on the base of the prementum.

*Elateridae* (pl. 6, H).

The labium of the *Elateridae* shows externally two distinct parts, the first prementum (*IPrmt*) and the postmentum (*Pmt*), but upon dissection there is found a third division, the second prementum (*IIPrmt*). This latter subdivision is firmly united with the first prementum but is completely invaginated into the distal end of the postmentum. Between the posterior margin of the postmentum and the posterior tentorial pits (*pt*) lie the closely approximated cardines (*Cd*) of the maxillae. Present also is a gular region (*Gu*) lying between and behind the tentorial pits.

There are two pairs of ventral muscles present in the labium of these larvae. The retractors of the prementum (*rst*) originate from the distal region of the postmentum. They insert on the ventral margin of the second prementum. The ventral adductors (*2adlb*) arise from the tentorial arms (*Tent*) and insert on the base of the first prementum.

*Passalidae* (pl. 6, F).

The labium of *Passalus* is made up of three distinct areas: the prementum (*Prmt*), the mentum (*Mt*), and the submentum, which is not separated from the gula and hence forms a combined region (*Gu+Smt*). The prementum carries, as usual, the palpi. The mentum is triangular and devoid of setae. It lacks the typical shape as found in adult beetles (pl. 1, C, *Mt*) since its anterolateral angles are not extended. There seems to be no membranous area between it and the prementum but the suture separating them undoubtedly allows flexibility. More than half the ventral surface of the labium consists of the submentum. The distal part is flanked by a pair of sclerites which are set off from the remainder of the region by sutures, but it is doubtful if they have any significance beyond being part of the submentum. Slightly behind the middle and somewhat removed from the lateral margins of the submentum are found the posterior tentorial pits (pl. 6, F, *pt*), from which arise the internal tentorial bridge (*Tent*).

The ventral muscles are only one pair, the ventral adductors of the labium (*zadlb*). They arise from the tentorial bridge and insert on the base of the prementum.

*Scarabaeidae* (pl. 6, E).

In *Ochrosidia* we have a three-part labium made up of a first prementum which has two pairs of setae, a second prementum bearing one pair of setae, and the postmentum, likewise having one pair of rather large setae. The divisions are readily distinguished by a membranous area between the first two and a flexible suture between the second prementum and the postmentum.

The ventral adductors of the labium (*zadlb*) arise from the tentorium (*Tent*) on the remnants of the posterior tentorial arms (pl. 8, G, *PT*). They insert on the base of the first prementum (pl. 6, E, *IPrmt*). The retractors of the prementum (*rst*) arise on the postmentum near the midline and insert on the base of the second prementum (*IIPrmt*). They are slightly asymmetrical in that the right muscle is considerably stouter than its fellow. This is an adaptation, in *Ochrosidia*, to the unusually asymmetrical hypopharyngeal sclerotization.

*Melyridae* (pl. 6, G).

The labium of *Melyridae* consists of a rather insignificant first prementum (*IPrmt*), an elongate second prementum (*IIPrmt*), and an area lying completely between the posterior tentorial pits (*pt*) which would appear to be a combined postmentum and gula (*Pmt+Gu*).

The ventral labial muscles again consist of two pairs. The ventral adductors of the labium (*zadlb*) originate from the tentorial bar (*Tent*) and insert on separate sclerites in the small first prementum. The retractors of the prementum (*rst*) arise from the postmentum and insert beyond the middle of the elongate second prementum.

*Meloidae* (pl. 7, C).

The first prementum (*IPrmt*) and the second prementum (*IIPrmt*) are clearly set off from one another and from the remainder of the labium. The postmentum and gula (*Gu+Pmt*) form a continuously sclerotized area and neither one is to be easily differentiated from the other. Since the bases of the tentorial arms have become greatly elongated into low ridges the tentorial pits are not clearly marked and can not be used to separate the postmentum from the gula.

Corresponding to the division of the prementum there are two ventral pairs of muscles. The retractors of the prementum (*rst*) arise on the postmental area and insert on the base of the second prementum. The ventral adductors of the labium (*zadlb*) arise on the ridgelike tentorial arms and insert on the base of the first prementum.

*Cerambycidae* (pl. 7, A).

The labium of *Orthosoma* shows the divisions which are typical of adult Coleoptera and of Orthoptera (pl. 1, B, C): a distal prementum (pl. 7, A, *Prmt*), and a postmentum (*Pmt*) subdivided into a mentum (*Mt*) and a submentum (*Smt*).

The muscles of the labium consist of one ventral and one dorsal pair, the ventral adductors of the labium (*zadlb*) and the dorsal adductors of the labium (*iadlb*) respectively. They both have their origin on an extension from the tentorial bridge (*Tent*). The ventral adductors insert on the base of the prementum near the ventral midline. The dorsal adductors attach dorsally near the lateral margins of the base of the prementum.

*Bruchidae* (pl. 7, F).

The labium of *Spermophagus* shows a remarkable departure from the labia of coleopterous larvae in general in that the labial palpi are entirely lacking. The prementum (*Prmt*) simply ends bluntly. The first and second prementa are completely united, although the united region has two pairs of ventral muscles. The postmentum (*Pmt*) contains a sclerite which has a shape much resembling that of a new moon. The postmentum is considerably broader than the prementum and extends laterally nearly to the median margin of the cardo (*Cd*).



In common with the labia of Chrysomeloidea (see below) there are two ventral pairs of muscles. These are the ventral adductors of the labium (*2adlb*) and the retractors of the prementum (*rst*). As stated above, both pairs insert on the prementum, on the single sclerite. The retractors of the prementum also arise on the tentorial bridge lateral to the points of origin of the adductor muscles. They attach on the base of the sclerite of the prementum.

*Camptosomatidae* (*Cryptocephalinae*) (pl. 7, B).

The representative of this family which was used in the study has the labium very similar to that of Eumolpidae (see below). The labium shows a first prementum (*IPrmt*), and a considerably elongated second prementum (*IIPrmt*), the elongation apparently having resulted at the expense of the postmentum (*Pmt*), which is rather short and small.

The muscles are similar to those of the preceding family, both ventral pairs originating from the tentorium. The retractors of the prementum (*rst*) insert at a point considerably removed distally from the base of the second prementum. The ventral adductors of the labium (*2adlb*) are long and extend to the first prementum, where they insert on the base of that division.

*Eumolpidae* (pl. 7, E).

The labium of Eumolpidae shows a distinct division into three parts, the first prementum (*IPrmt*), the second prementum (*IIPrmt*), and the postmentum (*Pmt*). The first prementum bears the palpi. The second prementum has, near its base and closely approaching one another in the midline, a pair of sclerites, each of which bears a seta. There is no gula present, and the base of the postmentum connects directly with the neck membrane. The two halves of the head are firmly held together ventrally by the tentorial bar (*Tent*).

The ventral muscles consist of two pairs, the ventral adductors of the labium (*2adlb*), and the retractors of the prementum (*rst*). The former originate from the tentorium and insert on the sclerotized area at the base of the first prementum, near its lateral margins. The retractors of the prementum (*rst*) likewise arise on the tentorial bar but insert near the base of the second prementum on the sclerites referred to in the preceding paragraph.

*Galerucidae* (pl. 7, D).

In *Galerucella* the labium consists, apparently, of but two divisions, the first prementum (*IPrmt*) and the second prementum (*IIPrmt*). The first prementum carries the palpi and has across its base a narrow



sclerite on which two setae are situated near the midline. The second prementum (*IIPrnt*) makes up the major portion of the labium. Covering much of the median part of this division is a sclerite, near the anterior margin of which are located two setae. The postmentum has become reduced, even more so than in *Cryptocephalinae* (B), and does not show in the figure. The labium in this group is very prominent and protrudes from the ventral level of the head as a large flap. The postmentum has become adapted for connecting the posterior margin of the second prementum with the neck membrane and extends more or less vertically.

The ventral muscles consist of two pairs, the ventral adductors of the labium (D, *2adlb*) and the retractors of the prementum (*rst*). The former originate from the tentorium (*Tent*) and insert on the sclerite at the base of the first prementum. The retractors also arise from the tentorium, medially to the origin of the ventral adductors, and insert in about the center of the sclerite of the second prementum.

### III. THE TENTORIUM OF COLEOPTEROUS LARVAE

The tentorium of insects in general is of considerable interest, and a few examples of the structure as found in coleopterous larvae are included here. The probable evolutionary development of this internal "skeleton" has been given by Snodgrass (1935) and no repetition of the present-day views will be included in this paper.

The tentorium of apterygote insects at least is composed of two pairs of braces or arms. One pair consists of invaginations from the anterior tentorial pits. The second pair of arms results from invaginations from the posterior tentorial pits. These component parts may be united in various ways, as Snodgrass has shown (1935, fig. 62), or the four parts may be entirely separate and greatly reduced. Oftentimes there is, in addition to the two pairs of arms above mentioned, a third pair of dorsal arms. These, however, are considered to be secondary outgrowths of the anterior arms and not invaginations from the dorsal wall of the head, since their connection with the head is usually membranous or at times entirely lacking.

In addition to its function of bracing the walls of the head, the tentorium serves as a very important region for muscle attachments. From it usually originate the adductor muscles of the maxillae and the labium, the retractors of the hypopharynx and the ventral dilators of the stomodaeum. The antennal muscles are also attached to the tentorium, usually to the dorsal arms when present.

Of the tentoria of coleopterous larvae which were studied, that of *Silpha* is the most nearly similar to the generalized type. The pos-

terior arms (pl. 8, A, B, *PT*) arising from the posterior tentorial pits are closely approximated at their bases, but as they proceed anteriorly and dorsally, they diverge somewhat. Also, they are continued posteriorly beyond the pits. On this posterior extension are attached the ventral dilators of the pharynx, and on it also are inserted the ventral muscles which extend from the prothorax into the head. United with the distal ends of the posterior arms are the anterior tentorial arms (pl. 8, B, *AT*). The dorsal arms (B, *DT*) originate from the anterior arms and extend dorsally to the head wall. The lateral elements, each consisting of a posterior, anterior, and dorsal arm, are not united across the median line in *Silpha*.

In *Merinus laevis* (C) the posterior arms (*PT*) have lost connection with the anterior arms. They are short and have broadened out into rather flat plates, which, although close together in the midline, are completely separate. On these arms are attached at least the ventral adductors of the labium (pl. 5, C, *2adlb*).

*Tenebroides* (pl. 8, D) shows a condition very similar to that of *Merinus*, the posterior arms (*PT*) being separate and not connected with the anterior arms.

The posterior tentorium of *Synchroa* (E, F, *PT*) consists merely of a transverse bar between the posterior tentorial pits and is somewhat concave ventrally. No projections or extensions, which might indicate connection with the anterior arms are observable. On the transverse bar are attached the ventral adductors of the labium.

A somewhat similar case to the above is found in *Ochrosidia villosa* (G, H) where the tentorium consists essentially of a bridge. It is, however, not invaginated into the head but is continuous with the lateral walls in such a manner as to form a smooth arch. From the inner dorsal margin of this bar two extensions (G, H, *PT*) arise which are evidently parts, at least, of the posterior tentorial arms. On these are attached the strong adductor muscles of the maxillae and the ventral adductors of the labium (pl. 6, E, *2adlb*).

The posterior tentorial apparatus of the staphylinid larva, *Hesperus baltimorensis* (I, J), is made up of two Y-shaped structures, the base of the Y being directed ventrally and connected with the posterior tentorial pits. These lateral elements are completely separated. On the base of each is attached its corresponding portion of the ventral adductors of the labium.

In *Cicindela* (K) the lateral elements of the posterior tentorium have grown together at their bases, and there has resulted a flat transverse plate extending nearly perpendicularly into the head. The inner ends are slightly separated, which indicates that the tentorium, as it

is at present, has resulted from a coalescing of what was originally two posterior arms.

The tentorium of coleopterous larvae, although it may show various forms, can be homologized with the primitive structure, as has been shown above.

#### IV. CONCLUSION

The muscles of the head capsule of the larvae of Coleoptera conform, for the most part, with those of a generalized insect such as the roach. There are, of course, various modifications which have taken place in connection with the habits of the particular species. The ligula, when present, was not observed to be divided into glossae or paraglossae in any case, as it is in the orthopteroid insects. There were found no larvae that showed a typical hypognathous head, all the forms having the prognathous type, which has resulted in a conspicuous elongation of the postmentum or in the addition of a gular region behind the base of the labium. In some cases the postgenae have completely united, and this has caused a lengthening of the ventral wall of the head.

From the study thus far it does not appear that any particular form of labium is more generalized than another. It seems, however, that the labium of *Byrrhus* or of *Silpha* is typical. This type of labium consists of a prementum subdivided into a first and second prementum, and of a postmentum made up of only one division or sclerite. Too much emphasis should not be placed upon sclerites as indices of primary morphological areas, since they are but the result of secondary hardening processes in the integument; but until some better method is devised for delimiting or describing a part of the insect it is essential that they be used. When they are studied together with muscle origins and insertions, they become fairly safe criteria for separating parts of the external anatomy.

The tentorium of the larvae studied shows various modifications and specializations, but by means of a comparative study it may be homologized with the conditions as found in the more generalized insects.

## ABBREVIATIONS USED ON THE FIGURES

<i>ACd</i> , apodeme of cardo.	<i>LbPlp</i> , labial palpus.
<i>adcd</i> , adductor of cardo.	<i>Lig</i> , ligula.
<i>adlb</i> , adductor of labium.	<i>lplp</i> , labial palpus.
<i>adst</i> , adductor of stipes.	<i>MAnt</i> , antennal muscle.
<i>AT</i> , anterior arm of tentorium.	<i>Mt</i> , mentum.
<i>at</i> , anterior tentorial pit.	<i>Pgl</i> , paraglossa.
<i>b</i> , secondary sclerite of prementum in <i>Periplaneta</i> .	<i>Plp</i> , palpus.
<i>Cd</i> , cardo.	<i>Pmt</i> , postmentum.
<i>Cvx</i> , neck, cervix.	<i>pos</i> , postoccipital suture.
<i>dplp</i> , depressor of palpus.	<i>Prmt</i> , prementum.
<i>DT</i> , dorsal arm of tentorium.	<i>IPrmt</i> , anterior subdivision of prementum.
<i>fgl</i> , flexor of glossa.	<i>IIPrmt</i> , posterior subdivision of prementum.
<i>For</i> , foramen magnum.	<i>PT</i> , posterior arm of tentorium.
<i>fppl</i> , flexor of paraglossa.	<i>pt</i> , posterior tentorial pit.
<i>Gl</i> , glossa.	<i>rhph</i> , retractor of hypopharynx.
<i>gs</i> , gular suture.	<i>rst</i> , retractor of prementum.
<i>Gu</i> , gula.	<i>Smt</i> , submentum.
<i>gu</i> , much narrowed gula.	<i>St</i> , stipes.
<i>HB</i> , hypopharyngeal bracon.	<i>TB</i> , cross bar of tentorium.
<i>Lb</i> , labium	<i>Tent</i> , tentorium.

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## EXPLANATION OF PLATES

## PLATE 1

- A. Internal view of hypothetical labium showing origins and insertions of all labial muscles.
- B. *Periplaneta americana* L. (adult). External view of muscles of labium.
- C. *Harpalus* sp. (adult). External view of muscles of labium.
- D. *Byrrhus* sp. (larva). External view of muscles of labium.

## PLATE 2

- A. *Cicindela hirticollis* Say (larva). Ventral view of labium.
- B. *Cicindela hirticollis* Say (larva). Ventrolateral view of left tentorial muscles of labium and hypopharynx.
- C. *Harpalus* sp. (larva). Ventral view of labium.
- D. *Amphizoa (insolens* Lec.)? (larva). Ventral view of labium.
- E. *Dytiscus* sp. (larva). Ventral view of labium.
- F. *Dinectes* sp. (larva). Ventral view of labium.

## PLATE 3

- A. *Silpha* sp. (larva). Ventral view of labium.
- B. *Hesperus baltimorensis* Grav. (larva). Ventral view of labium.
- C. *Hololepta* sp. (larva). Ventral view of labium.
- D. *Hydrous triangularis* Say (larva). Ventral view of labium.
- E. *Languria laeta* Lec. (larva). Ventral view of labium.
- F. *Cucujus clavipes* Fab. (larva). Ventral view of labium.
- G. *Oryzaephilus surinamensis* (L.) (larva). Ventral view of labium.
- H. *Eumaisibius wheeleri* Schwartz and Barber (larva). Ventral view of labium.

## PLATE 4

- A. Nitidulidae (larva). Ventral view of labium.
- B. Endomychidae (larva). Ventral view of labium.
- C. *Mycetophagus* sp. (larva). Ventral view of labium.
- D. *Tritoma unicolor* Say (larva). Ventral view of labium.
- E. *Anthicus* sp. (larva). Ventral view of labium.
- F. *Byrrhus (unicolor* Say)? (larva). Ventral view of labium.
- G. Colydiidae (larva). Ventral view of labium.

## PLATE 5

- A. *Synchroa punctata* Newm. (larva). Ventral view of labium.
- B. *Dendroides bicolor* Newm. (larva). Ventral view of labium.
- C. *Merinus laevis* (Oliv.) (larva). Ventral view of labium.
- D. *Pytho* sp. (larva). Ventral view of labium.
- E. *Hymenorus* sp. (larva). Ventral view of labium.
- F. Lagriidae (larva). Ventral view of labium.
- G. *Byrrhus* sp. (larva). Ventral view of labium.
- H. *Prionocyphon discoideus* (Say) (larva). Ventral view of labium.

## PLATE 6

- A. *Nosodendron* sp. (larva). Ventral view of labium.
- B. *Ptilodactyla serricollis* (Say) (larva). Ventral view of labium.
- C. *Chauliognathus* sp. (larva). Ventral view of labium and maxillae.
- D. *Cebrio* sp. (larva). Ventral view of labium.
- E. *Ochrosidia villosa* (Burm.) (larva). Ventral view of labium.
- F. *Passalus cornutus* F. (larva). Ventral view of labium.
- G. Melyridae (larva). Ventral view of labium.
- H. *Melanotus* sp. (larva). Ventral view of labium.

## PLATE 7

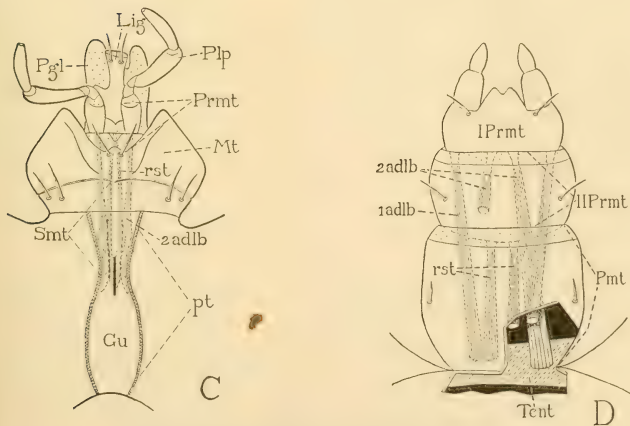
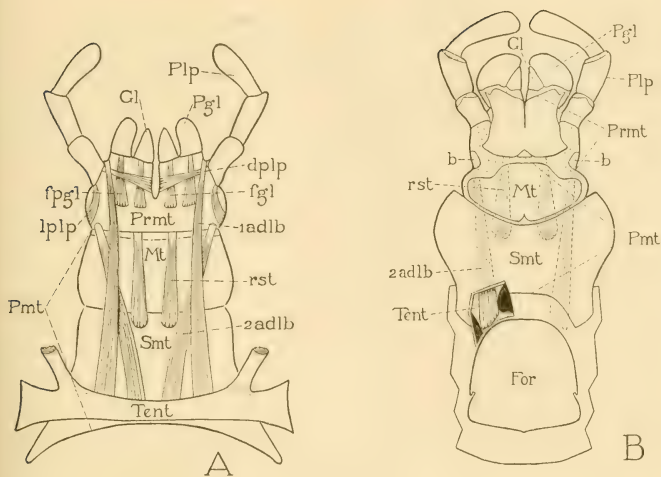
- A. *Orthosoma* sp. (larva). Ventral view of labium.
- B. Camptosomatidae (Cryptoccephalinae) (larva). Ventral view of labium.
- C. *Henous confertus* Say (larva). Ventral view of labium.
- D. *Galerucella* sp. (larva). Ventral view of labium.
- E. Eumolpidae (larva). Ventral view of labium.
- F. *Spermophagus robinæ* Sch. (larva). Ventral view of labium and maxillae.

## PLATE 8

- A. *Silpha* sp. (larva). Dorsal view of posterior tentorium.
- B. *Silpha* sp. (larva). Lateral view of left half of tentorium.
- C. *Merinus laevis* (Oliv.) (larva). Dorsal view of posterior tentorium.
- D. *Tenebroides mauritanicus* (L.) (larva). Dorsal view of posterior tentorium.
- E. *Synchroa punctata* Newm. (larva). Dorsal view of posterior tentorial bar.
- F. *Synchroa punctata* Newm. (larva). Tentorial bar and postmentum cut in the midline.
- G. Cetoninae (larva). Dorsal view of posterior tentorial bridge.
- H. Cetoninae (larva). Tentorial bridge cut through the midline.
- I. *Hesperus baltimorensis* Grav. (larva). Dorsal view of posterior tentorium.
- J. *Hesperus baltimorensis* Grav. (larva). Lateral view of one of the elements of the posterior tentorium.
- K. *Cicindela* sp. (larva). Anterodorsal view of posterior tentorium.

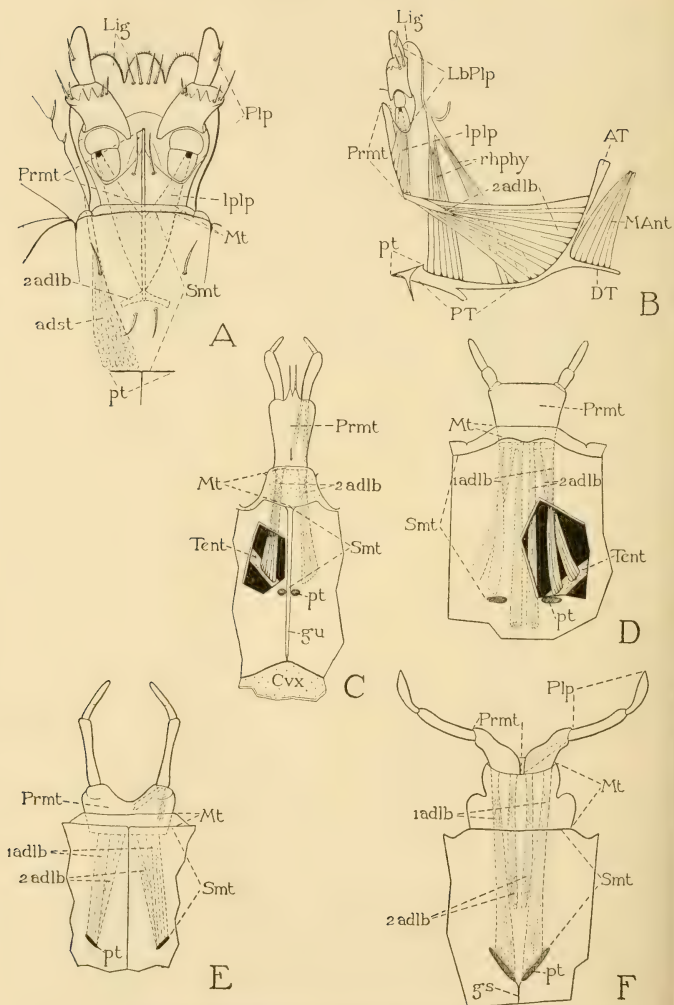






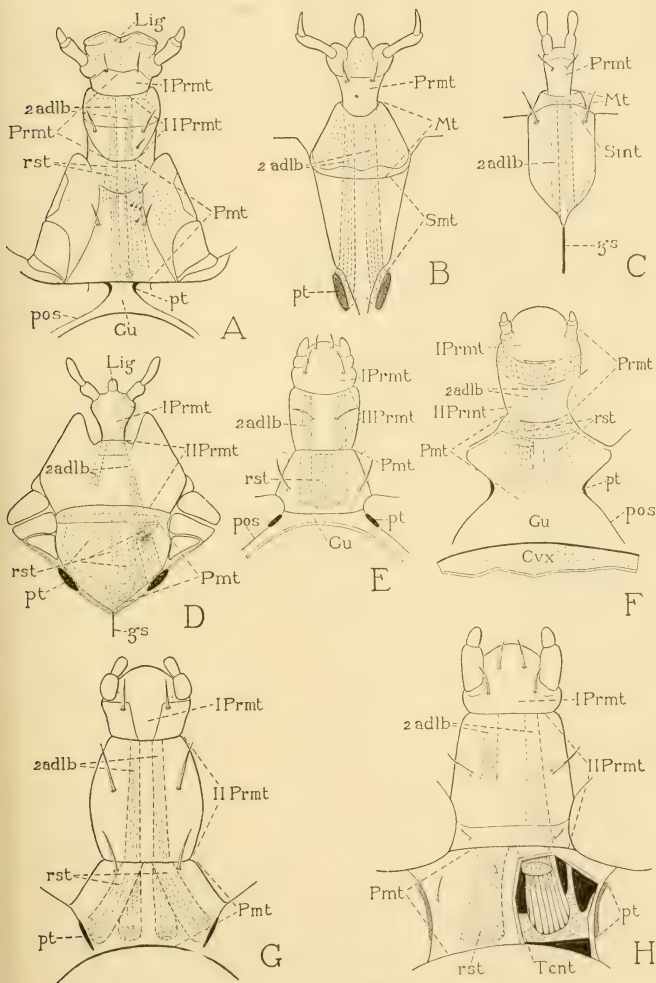
THE LABIUM OF COLEOPTEROUS LARVAE

(For explanation, see page 28.)



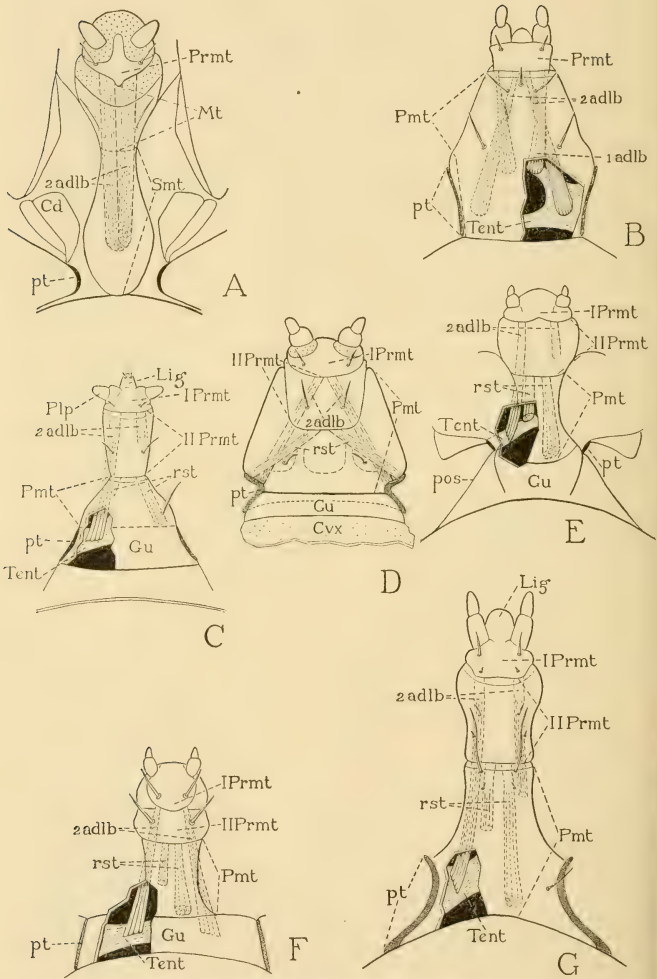
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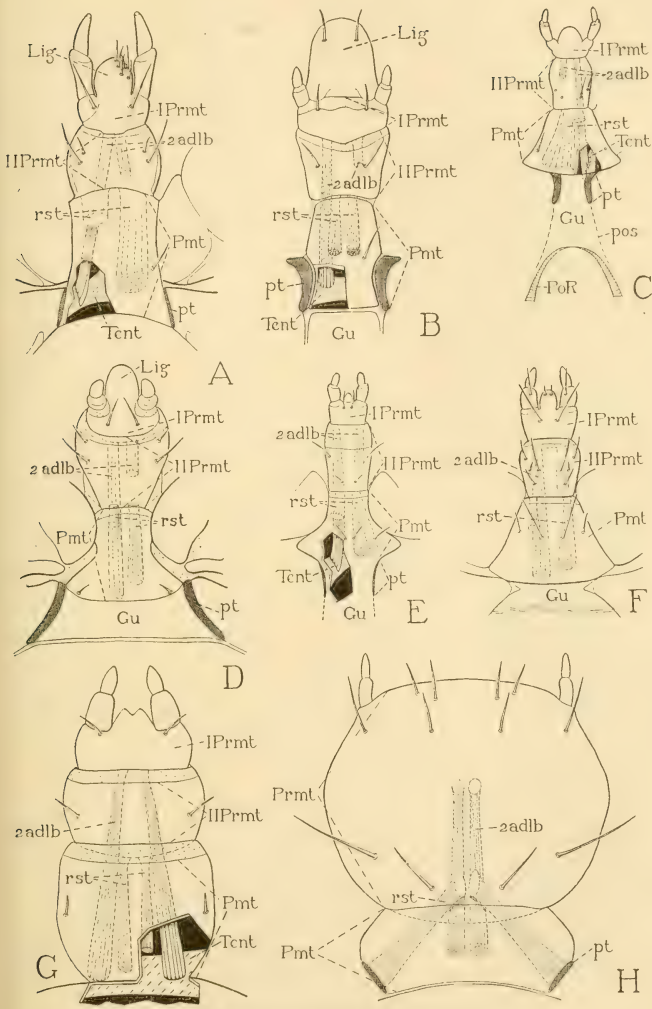
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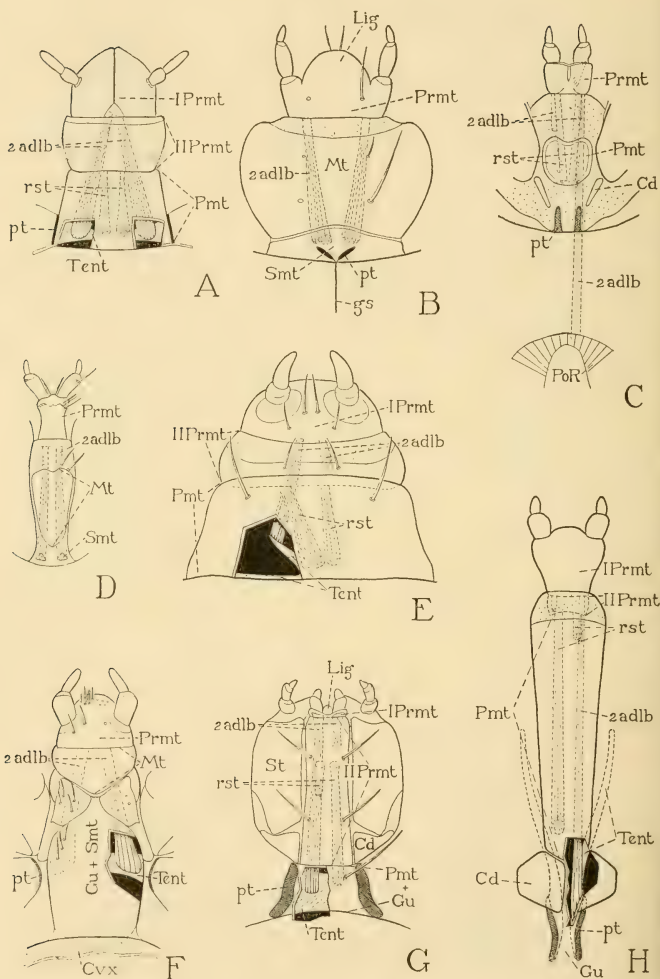
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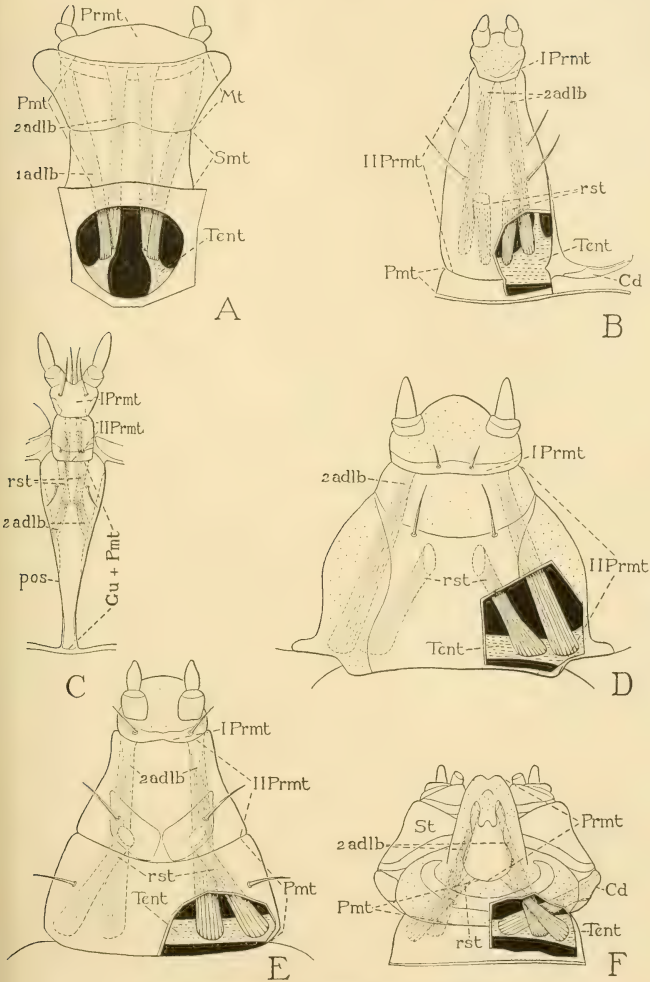
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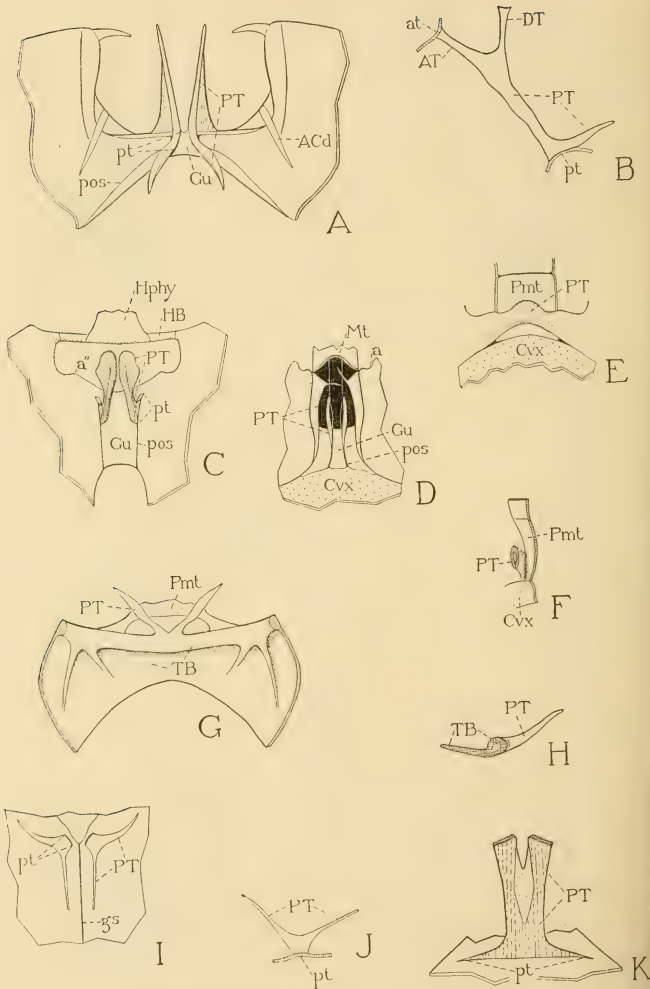


THE LABIUM OF COLEOPTEROUS LARVAE

(For explanation, see page 29.)



THE LABIUM OF COLEOPTEROUS LARVAE  
(For explanation, see page 29.)



THE TENTORIUM OF COLEOPTEROUS LARVAE  
(For explanation, see page 29.)

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 14

# MORPHOLOGY OF THE INSECT ABDOMEN

## PART III. THE MALE GENITALIA

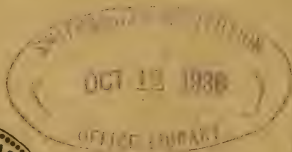
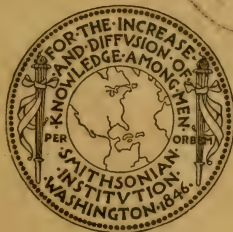
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BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine

U. S. Department of Agriculture.

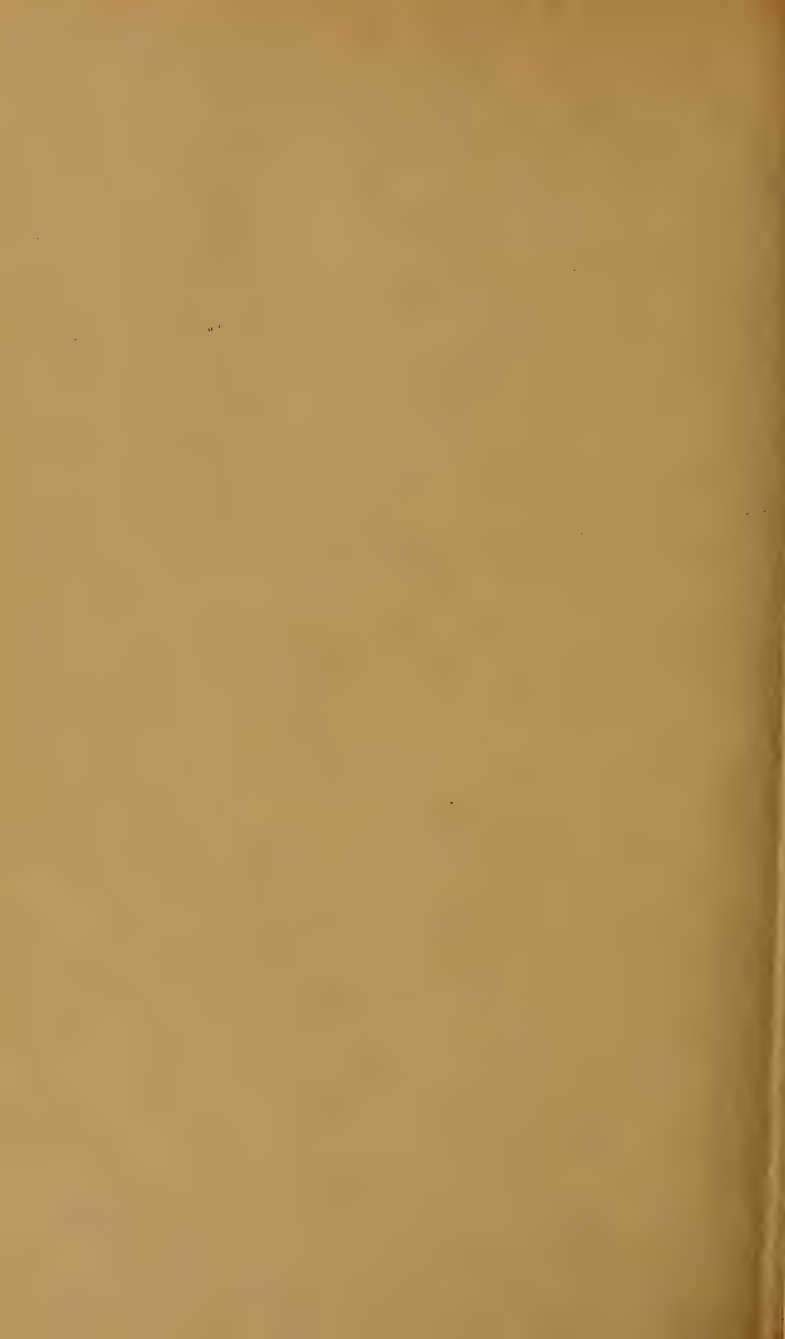


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### I. INTRODUCTION

The series of papers entitled "Morphology of the Insect Abdomen" is concluded with the present contribution. Other papers on the male genitalia of insects, however, are designed to follow. The only excuse here offered for the obvious fact that Part III, on the one hand, greatly exceeds the scope of the general title, and, on the other, leaves much to be said about insect genitalia, is the writer's conviction that insects must be studied morphologically as arthropods—a practice at least not prevalent among entomologists. The literature of entomological morphology is replete with long discussions on the nature and

evolution of insect structures that unquestionably might be brought to more satisfactory conclusions if entomologists could get over the habit of thinking of insects purely as insects. Since insects are arthropods, a wider survey of the general field of arthropod anatomy will often lead to a better understanding of things about insect structure than can be derived from an intensive study of the insects themselves. For this reason the present paper, which has for its object an understanding of the fundamental nature of insect genitalia, includes a review of the genital organs in the major groups of the Arthropoda and, for good measure, also in the Onychophora.

The somatic adaptations of animals to the function of reproduction are in general of a superficial nature; they have not brought about the development of any fundamental organ or system of organs comparable with the structures that subserve most of the other important activities of the animal, such as locomotion, orientation, alimentation, or blood circulation. This condition evidently arises from the fact that the germ cells, in a physiological sense, are parasites of the soma; though they are given lodgment within the body, the accommodations for their growth and discharge have been built up by alterations of structures already present for some other purpose, or by the addition of rather haphazard accessories. In the annelid-onychophoran-arthropod series of animals the only common feature of the reproductive system is the inclusion of the primary germ cells in the mesoderm. The germ cells liberated from the mesoderm are never discharged directly to the exterior through the ectoderm, as in some of the Coelenterata; they are first given off internally, usually into the coelome or confined parts of the latter, where they undergo their development into ova or spermatozoa, and the gametes must then be extruded from the body cavity to the outside through openings in the body wall. The evolution of the reproductive organs in the Arthropoda has been largely a matter of developing special containers for the maturing germ cells and of establishing exit passages for the gametes. External accessories have been added in most groups to assure insemination of the female by the male or to aid the female in the deposition of the fertilized eggs.

#### ENUMERATION OF THE ARTHROPOD BODY SEGMENTS

Because of the great variation in the position of the genital openings in the Arthropoda, it becomes highly desirable, in a comparative study of the external genitalia, to be able to identify and briefly designate the corresponding body segments in the several arthropod groups.

To enumerate the segments consecutively would not be a difficult matter were it not for the uncertainty, or difference of opinion at least, concerning the number of somites that enter into the composition of the head. The discrepancy of opinion arises principally from a difference of interpretation concerning "segmentation" in the cephalic region anterior to the somite of the tritocerebral brain lobes. This somite carries the second antennae, or chelicerae, and is without question postoral in its origin, though its lateral parts may lap forward at the sides of the mouth and its appendages thus acquire a preoral position in the adult. The head region anterior to the tritocerebral somite, often called the *acron* in the embryo, has been supposed to include an antennal, a preantennal, and even a labral somite, the evidence adduced being the presence of corresponding coelomic sacs in the mesoderm associated with ganglionic centers of the ectoderm innervating the sensory and appendicular organs of the acronal region. The first antennae (antennules) are the procephalic appendages most commonly present in the arthropods, and the antennae of Onychophora would appear to be their homologues in this group of related animals; but the embryonic position of the antennae relative to the mouth is variable, in some cases the appendages are preoral, in others adoral, and in others again they are slightly postoral.

Segmentation in the articulate animals is closely associated at least with the formation of paired coelomic sacs in the mesoderm. In the embryology of the annelids, as is well known, the coelomic mesoderm usually takes its origin from a pair of teloblastomeres situated at first behind the blastopore. From these cells are proliferated forward in the ventrolateral parts of the body of the larva two bands of mesoderm, in which there may be formed several pairs of primary coelomic cavities. The secondary somites of the worm added during or after metamorphosis are generated from a zone of growth situated between the last larval somite and the small terminal region of the body containing the anus (periproct, pygidium, telson). The mesoderm of the postlarval somites is in most cases proliferated also from the primary mesodermal teloblastomeres, though in some it is said to have its source in the teloblastic ectoderm (Iwanoff, 1928). The forward growth of the mesoderm bands in the Annelida is arrested at the mouth of the larva, and the first pair of coelomic cavities lies just behind the mouth; as a consequence there remains anterior to the mouth an unsegmented region of the trunk, known as the prostomium (fig. 1 A, *Prst*). With later development, however, the interior of the prostomium may become completely occupied by extensions of the

coelomic cavities of the first postoral somite (*PMsd*), and the prostomial walls may thus be lined by a coelomic peritoneum (see Meyer, 1901; Sokolow, 1911). The external organs of the prostomium in the Polychaeta include tentacles, palpi, eyes, and nuchal organs, but the cephalic coelome of the annelids is not known to be divided into corresponding sacs.

The coelomic mesoderm bands of the Onychophora also are teloblastic in their origin. Though they cannot be traced from a single

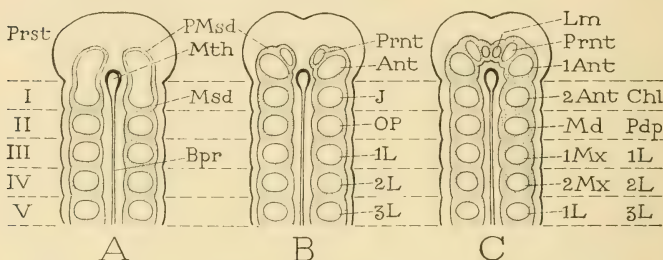


FIG. 1.—Diagrams showing the maximum observed development of the coelomic mesoderm in the anterior part of the trunk in Annelida, Onychophora, and Arthropoda, and the apparent homologies of the postoral somites.

A, Annelida: the coelomic sacs of mesoderm bands primarily all postoral, but the prostomium may be invaded by extensions of the coelomic sacs of first postoral segment. B, Onychophora: the coelomic mesoderm bands extend into the preoral region and here contain antennal and possible preantennal coelomic sacs (Evans, 1902). C, Arthropoda: the coelomic mesoderm bands may unite before the mouth and contain antennal, preantennal, and labral coelomic sacs (*Carausius*, Wiesmann, 1926).

*Ant*, coelomic sac of antenna; *1Ant*, same of first antenna (antennule); *2Ant* (*Chl*), same of second antenna or chelicera; *Bpr*, blastopore; *Chl* (*2Ant*), coelomic sac of chelicera or second antenna; *I-V*, coelomic sacs of first five somites; *J*, coelomic sac of onychophoran jaw somite; *L*, coelomic sacs of leg somites; *Lm*, coelomic sac of labral region; *Md* (*Pdp*), same of mandible or pedipalp; *Msd*, coelomic mesoderm; *Mth*, mouth; *1Mx*, *2Mx*, coelomic sacs of first and second maxillae, or of first and second legs of Chelicerata; *OP*, coelomic sac of oral papilla; *Pdp* (*Md*), same of pedipalp or mandible; *PMsd*, prostomial mesoderm; *Prst*, prostomium.

pair of teloblastomeres, they are generated from a multicellular germinal area of the blastoderm lying behind the blastopore. In their forward growth, however, the mesoderm bands of the Onychophora do not stop at the mouth; they extend into the head region anterior to the mouth (fig. 1 B) and are here excavated by a pair of large coelomic cavities (*Ant*) associated with the antennae, and possibly (Evans, 1902) by a pair of small transitory preantennal sacs (*Prnt*). Though the antennae and their nerve centers in the Onychophora lie well before the mouth, the antennal coelomic sacs are morphologically

adoral rather than preoral, since their posterior ends embrace the stomodaeum and give rise to the stomodaeal musculature (Kennel, 1888; Evans, 1902). The first truly postoral coelomic sacs of the Onychophora are those of the jaws (*J*); the next pertain to the oral papillae (*OP*).

Among the Arthropoda a teloblastic origin and growth of the coelomic mesoderm occurs in a sufficient number of cases (in certain Crustacea and Chilopoda) to suggest that it is the primitive method of mesoderm formation in this group as well as in the Annelida and Onychophora. The mesoderm bands extend into the procephalic lobes of the head as in adult Annelida and Onychophora, and may become here excavated not only by antennal (antennular) and preantennal coelomic sacs (fig. 1 C, *1Ant*, *Prnt*), but also, according to the observations of Wiesmann (1926) on *Carausius morosus*, by a pair of sacs in the labral region (*Lm*) lying immediately before the mouth. The preantennal and antennal sacs in this case, it should be observed, do not intervene between the labral sacs and the mouth, and are therefore not preoral; they lie at the sides of the mouth and are hence *adoral*. The labral sacs (or perhaps ocular sacs), on the other hand, are literally preoral, being adjacent to each other before the mouth. We may conclude, therefore, that in the Arthropoda, as in the Annelida, the coelomic mesoderm potentially surrounds the blastopore by the union of the mesoderm bands before the mouth, and that the antennal, preantennal, and labral coelomic sacs, when present, lie on adoral and preoral radii centering in the mouth (fig. 1 C). Whether these radial cavities of the mesoderm are to be called "somites" or not becomes largely a matter of definition. If the presence of a pair of cavities in the mesoderm associated with a pair of external organs and their ganglia is taken to define a segment, we may claim that the acron of the arthropods is potentially a segmented region. On the other hand, if a segment is conceived to be an independently movable section of the trunk, then there is no segmentation of the arthropod trunk anterior to the somite of the second antennae, shown either in the embryonic procephalon or in the corresponding part of the adult head capsule. According to Sollaud (1923), the first intersegmental groove in the embryo of Palaemoninae separates an anterior head region, or acron, from the first somite, which latter carries the second antennae. The crustacean acron, or preoral region of the embryonic head bearing the eyes and the first antennae, Sollaud believes, corresponds with the annelid prostomium. If this be true, it must be admitted that the prostomial region of an onychophoran (fig. 1 B)



or an arthropod (C) is invaded by the coelomic mesoderm, and may contain one, two, or three pairs of coelomic sacs.

According to this view, the preantennae and antennules of the Arthropoda are comparable with the prostomial tentacles and palpi of the Polychaeta, and the absence of individual coelomic sacs associated with the cephalic appendages of the latter may be attributed to the imperfect development or more primitive condition of the prostomial mesoderm in the annelids. The known facts of comparative embryology show clearly that the "segmentation" of the preoral mesoderm is highly variable, and it is perhaps significant that the most complete example of it has been found in an insect. In any case, the idea that the prostomium, or acron, of the articulate animals is a preoral trunk region inherently devoid of coelomic mesoderm is evidently a fallacious concept based on the condition in the specialized trochophore larva of polychaete annelids and other invertebrates. There would seem to be no morphological reason why the mesoderm bands should not encircle the blastopore, surrounding the mouth anteriorly as they do the anus posteriorly. On this theory it is easy to accept the claim of histoneurologists that the oculo-antennal part of the arthropod brain (protocerebrum and deutocerebrum) corresponds with the prostomial brain of the annelids, and that the second antennal brain lobes represent the ganglia of the first postoral somite.

Following the concept thus developed that the first antennal and preantennal coelomic sacs, when present in the Arthropoda, are primarily adoral in position and lie in a region of the head (the acron) corresponding with the prostomium of an annelid, the entirely practical plan is here adopted of designating numerically the truly postoral segments beginning with the tritocerebral somite as *Segment I* (fig. 1 C, I). The appendages of this segment are the second antennae of Crustacea, the chelicerae of Chelicerata (C, 2*Ant*, *Chl*), or the corresponding embryonic rudiments of these organs found in many Hexapoda. In any case, there is no doubt as to the identity of the tritocerebral somite, and there is no question that it is the *first postoral segment of the adult* in all the Arthropoda.

Some of the arthropods are *epimorphic*, the definitive number of body segments in such forms being established at the end of embryonic development; others are *anamorphic*, in which case either a fixed or an indefinite number of segments is added during postembryonic growth. The generation of new segments appears always to take place at one point, which is a zone of growth located between the last-formed somite and the terminal periproct, or telson. The occurrence of anamorphosis is well known in Crustacea, Diplopoda, Chilopoda.

and Protura; the process of segment formation has been followed in detail by Pflugfelder (1932) in a diplopod. If the generation of arthropod somites is invariably teloblastic, it would seem to follow that the numerical order of a segment in the body series of any arthropod would determine the homology of this segment with a segment of the same number in any other arthropod. This principle, however, does not apply to the anterior segments, since in the development of both the annelids and the arthropods there is a primary body region that becomes itself differentiated into a small number of somites. With the Polychaeta the first few body somites are formed directly in the hyposphere of the trochophore; the nauplius larva of Crustacea has a short body region containing two primary somites (second antennal and mandibular), the succession of secondary teloblastic somites beginning with the segment of the first maxillae. (See Iwanoff, 1928; Sollaud, 1923.)

#### ORIGIN OF THE GONADS AND THE GONODUCTS

The groups of primary germ cells that occur in the mesodermal tissues are known to students of the Annelida as the "gonads", and they are appropriately thus termed since the word means a "sprout" or "germinating bud". These germ cell groups of the annelids, however, correspond with the so-called "germaria" of the Arthropoda, and in arthropod anatomy the term "gonad" refers to the mesodermal sac that contains the germinal cells in its epithelial walls. This nomenclatural confusion is unfortunate, and it is difficult to remedy. For an arthropodist it is easier to use the term *germarium* in a general sense to include the annelid "gonads", and to retain the name *gonad* for the mesodermal sacs (ovaries or testes) that contain the *germaria*—a usage generally followed in zoology.

In the Annelida the primary germ cells are early localized in the coelomic epithelium, where, as they multiply, they form small cell masses, which may occur most anywhere in the coelomic walls or may be limited to definite areas of particular segments. The germ cells given off from the germarial centers undergo their development in the coelomic cavities or in coelomic pouches. In some forms the sex elements escape through temporary openings in the body wall, in others the posterior part of the body containing them is constricted off, but more generally they make their exit through special genital outlets, or through modified nephridia.

In the Onychophora the germarial centers of the embryo are located in the splanchnic walls of the mesoderm above the alimentary canal

in one or several somites near the posterior end of the body (fig. 2 A, *Grm*). The dorsal parts of the coelomic sacs of these segments (figs. 2 B, 3 A, *a*) become constricted from the lateral parts (*b*) forming a series of gonadal pockets containing the germ cells. At a cor-

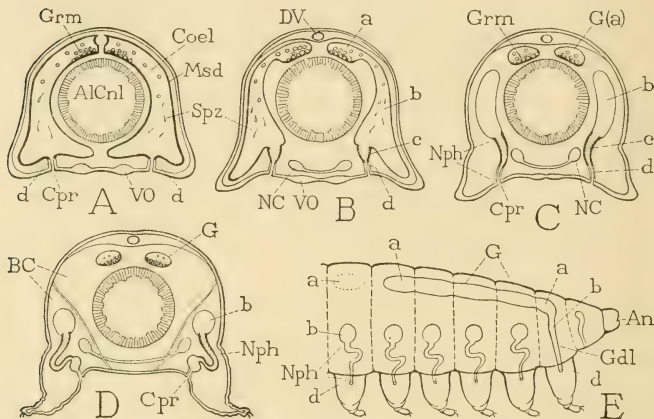


FIG. 2.—Diagrams showing the development of the gonads, gonoducts, and nephridia of Onychophora from coelomic sacs and coelomoducts (based on Kennel, 1888, Sedgwick, 1885, Evans, 1902).

A, cross-section of body segment at theoretical phylogenetic stage represented by embryo with complete coelomic sacs (*Coel*) and coelomoducts (*d*), germaria (*Grm*) dorsal in splanchnic walls of coelomic sacs, gametes (*Spz*) discharged through coelomoducts. B, later stage with gonadal pouches (*a*) constricted from lateral compartments (*b*) of coelomic sacs. C, still later stage, gonadal pouches (*B, a*) converted into gonadal sacs (*G*), lateral coelomic compartments (*b*) connected with coelomoducts, which have become nephridia (*Nph*). D, mature condition, gonads (*G*) a pair of dorsal tubes, lateral coelomic compartments (*b*) reduced to small end-sacs of nephridia. E, longitudinal section, showing gonad connected with lateral gonoduct (*Gdl*) formed of reduced coelomic sac of penultimate somite, which has maintained its continuity and has not been converted into a nephridium.

*a*, dorsal pouch of coelomic sac; *AlCnl*, alimentary canal; *An*, anus; *b*, lateral compartment of coelomic sac; *BC*, definitive body cavity; *c*, ventral diverticulum of coelomic sac; *Coel*, coelomic sac; *Cpr*, coelomopore; *d*, ectodermal part of coelomoduct; *DV*, dorsal blood vessel; *G*, gonad; *Gdl*, lateral gonoduct; *Grm*, germarium; *Msd*, mesoderm; *NC*, nerve cord; *Nph*, nephridium; *Spz*, spermatozoa; *VO*, ventral organ of ectoderm.

responding phylogenetic stage, it is to be presumed, the gametes (fig. 2 A, B, *Spz*) were liberated into the coelomic sacs and discharged through the open coelomoducts (*c, d*) of the latter. In the developing embryo, however, the gonadal pockets are soon shut off entirely from the rest of the coelome (C), and those of each side unite with

each other in a continuous tube (E, G). The two tubes thus formed become the definitive gonads. The germaria are now parts of the epithelial walls of the gonadial tubes; consequently the germ cells given off from the germaria are imprisoned in the gonads, and must be given some special means of escape to the exterior.

The genital exits of the Onychophora are formed in the last of the series of genital segments, which is the penultimate body somite. In this somite the coelomic sacs are retained entire (fig. 3 B); though they become much narrowed, they are not divided into dorsal and lateral compartments as in the preceding somites (fig. 2 C). Their dorsal ends unite with the posterior ends of the gonadial tubes (fig. 2 E), and there is thus established a pair of exit passages from the gonads opening externally through the primitive coelomoducts (*d*) of the segment. In other words, a relatively generalized condition is retained in the last genital segment, which allows the gametes to be discharged in the primitive manner through the coelomic sacs and their outlet ducts. The open passages take on a tubular form and become the definitive lateral gonoducts. Eventually the lateral ducts (fig. 3 C, *Gdl*) come together medially on the ventral surface of the last genital segment, and those of the male open into an ectodermal gonoductus communis (*Gdc*), or ejaculatory duct (fig. 6 C, D, *Dej*).

Among the Arthropoda a direct development of the gonads and gonoducts from coelomic sacs in a manner similar to the development of these organs in the Onychophora has been described by Heymons (1901) in *Scolopendra*. The dorsal parts of the coelomic sacs of the centipede embryo persist as a double series of closed chambers, which unite on each side, thus forming two long tubes with segmental compartments, in the epithelial walls of which are contained the germ cells. Later the dissepiments disappear, giving each gonadial tube a continuous lumen, and finally the two tubes combine to form the single definitive gonad. The gonoducts of *Scolopendra* are derived from the coelomic sacs of the greatly reduced last two somites. Each of these sacs gives off a small ventral diverticulum, or ampulla (fig. 3 D, *Amp*), into the corresponding rudimentary appendage of its segment (*2Gp*). The two sacs on each side then combine in a single vessel, and the sacs of the first pair join with each other above the alimentary canal and unite here with the posterior end of the gonadial tube. The ampullae of the second pair of sacs now withdraw from the appendages and migrate toward the median line on the ventral body surface, where finally they open into a median ectodermal invagination formed behind the sternum of the small last somite. The passages thus established from the gonadial tube to the exterior constitute the gono-

ducts. (In the male of *Scolopendra* only the right duct becomes the functional genital exit.) By comparison with Onychophora, it seems very probable that the ventral ampullae of the genital coelomic sacs of *Scolopendra* represent rudiments of coelomoducts that formerly opened on the bases of the segmental appendages.

The coelomic origin of the gonads and gonoducts is shown also in the embryonic development of various other arthropods, particularly in the Chelicerata. Hence, it is to be inferred that in cases where the gonads and their ducts appear first as solid cell masses, as with the insects, that this condition is a secondary modification, and that the lumen subsequently formed in the organs represents a part of the coelome. In certain insects it has been observed that the solid strands of cells that become the lateral genital ducts end with hollow ampullae. These ampullae lie in the appendage rudiments of the seventh abdominal segment in the female, or in those of the tenth segment in the male; in some cases the duct branches to each of these segments (see Heymons, 1892, 1895; Wheeler, 1893). When no appendage rudiments are present the ducts usually end in the same respective segments.

Inasmuch as the coelomic sacs of insects are seldom perfect and their cavities soon become confluent with the haemocoel, the evidence from embryology in this case does not show that the genital ducts are formed from entire coelomic sacs. The gonads and gonoducts appear first as solid strands of cells in the splanchnic walls of the mesoderm. It seems quite possible, therefore, that gonoducts may be formed by the closure of channels in the coelomic walls leading from the germinal areas to the coelomic outlets, just as the gonads are derived from a series of coelomic pockets containing the germ cells.

It is often said that the gonoducts are "modified nephridia". The assertion may be true with respect to some of the Annelida, but evidently when applied to Onychophora and Arthropoda it is not a correct statement of the facts. An onychophoran nephridium is a segmental coelomoduct connecting a remnant of the lateral coelomic compartment of the same segment with the exterior (fig. 2 D, *Nph*). The excretory head glands of Crustacea are organs of the same type of structure. An onychophoran or chilopod gonoduct, as shown by its development in *Peripatus* and *Scolopendra* (fig. 3 B, D), represents an entire coelomic sac together with its exit tube. Hence, if a nephridium of the onychophoran type is once formed in a segment, it cannot be converted into a genital duct. The onychophoran nephridia, on the other hand, might be regarded as remnants of segmental gonoducts, if it be assumed that each coelomic sac primitively contained a



germarial area in its wall, of which there is no specific evidence. The erroneous idea that arthropod gonoducts are modified nephridia is probably in part a result of the different significance of the term "gonad" as used by students of Annelida and Arthropoda, but it is largely based on a failure to recognize the essential difference between

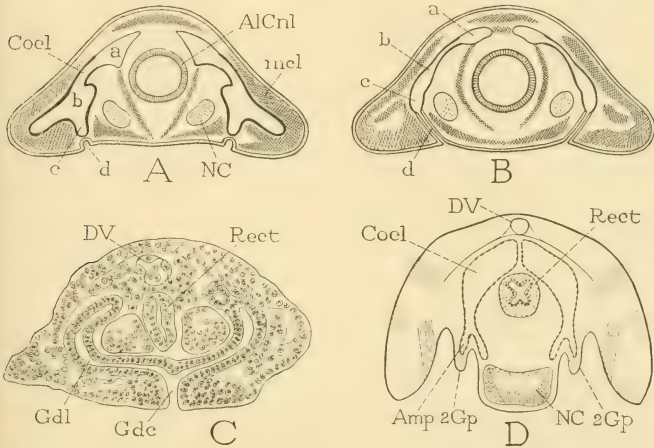


FIG. 3.—Development of the genital ducts in Onychophora and Chilopoda. (A, B from Kennel, 1888; C from Evans, 1902; D from Heymons, 1901.)

A, cross-section of a pregenital segment of *Peripatus*, diagrammatic, showing subdivision of the coelomic sacs and beginning of formation of coelomoducts (*c*, *d*). B, same through genital segment, showing formation of genital ducts from coelomic sacs and coelomoducts. C, section of genital segment of *Eoperipatus weldoni* with ectodermal gonoductus communis (*Gdc*) giving outlet to the lateral ducts. D, diagrammatic cross-section of genital segment of *Scolopendra* with coelomic sacs that will become genital ducts.

*a*, dorsal compartment of coelomic sac; *AlCnl*, alimentary canal; *Amp*, ampulla of coelomic sac in rudimentary gonopod; *b*, lateral compartment of coelomic sac; *c*, ventral diverticulum of coelomic sac; *Coel*, coelomic sac; *d*, ectodermal coelomoduct; *DV*, dorsal blood vessel; *Gdc*, gonoductus communis; *Gdl*, gonoductus lateralis; *Gp*, rudiment of gonopod; *incl*, muscle; *NC*, nerve cord; *Rect*, rectum.

an annelid nephridium and the organs given the same name in Onychophora and Crustacea. As shown by Goodrich (1895, 1897-1900), the nephridia and gonoducts of Annelida are probably distinct and separate structures in their origin; in the Polychaeta the genital ducts in most cases are either united with the nephridia or are reduced to ciliated lobes of the coelomic walls, in which case the nephridia may serve as genital outlets. In the Onychophora and Arthropoda, on the



other hand, true nephridia are never developed; but coelomoducts (perhaps primitive genital outlets) may be formed in each segment of the Onychophora, and it is these structures, together with remnants of the coelomic sacs, that give rise to the segmental excretory organs of Onychophora and Crustacea commonly termed "nephridia", and which form the definitive genital ducts of the Onychophora and Arthropoda in particular somites.

When the germ cells multiply and are extruded from the germaria in a genital organ of the arthropod type, they are received at once into the lumen of the mesodermal gonadial sac. The gonadial sac, or gonad, furnishes the germ cells a protected space within the body in which they may complete their development. With the multiplication and growth of the germ cells the gonad increases in size by an extension of its cellular walls, and it also assumes the rôle of nutritive organ for the developing ova or spermatozoa within it. Any specific part of the sac that contains and nourishes the growth stages of the gametes, therefore, constitutes a *trophocyst*, or *vitellarium*, of the ovary or testis.

The mature gonad may retain the form of a simple sac, in the walls of which the germinal cells may be diffusely scattered or localized at some particular place, but with many of the arthropods the capacity and productivity of the gonad are augmented by a secondary lobulation of the walls or by the outgrowth of saclike or tubular diverticula (sperm tubes or egg tubes), each containing a germinal area, usually at its blind end. In some of the apterygote insects the gonadial diverticula have a segmental arrangement, but generally there is no relationship between the germinal pockets of the gonads and the body segments. Both the ovary and the testis are primarily single organs in the embryo; though primitively they may have been formed from the germarial pockets of several consecutive coelomic sacs, the coelomic components have nothing to do with the subsequent outgrowth of follicular or tubular diverticula. Any theory of metamerism in the reproductive organs of the arthropods, therefore, must go back to a very early phylogenetic stage when the germinal centers were segmentally arranged in the coelomic walls, and the gametes were discharged through open coelomoducts connecting the coelomic sacs with the exterior. The only case among the arthropods of multiple genital openings and genital ducts associated with gonadial sacs occurs in the Pycnogonida, but the great reduction of the body and the branching of the gonad into the legs gives reason for suspecting that the genital apertures on the second leg segments of these animals (fig. 7, *Gpr*) are secondary formations. The pycnogonid gonad is said to be a

single organ at an early stage of its development. It is most unfortunate that we know nothing of the genital openings of the trilobites.

The great variation in the position of the genital outlets in different groups of arthropods is only to be explained on the assumption that quite different pairs of coelomic sacs have been utilized as genital ducts. This assumption might seem to imply that the various arthropod groups were differentiated from common ancestors that still retained a full series of coelomic sacs with exit ducts; but the idea is entirely incompatible with the identity in structure of the gonads in closely related groups that differ in the segmental position of the gonoducts, as in Entomostraca, Chilopoda, and Hexapoda. Moreover, in the geophilomorphic chilopods the genital ducts may pertain to different segments in different individuals of the same species, according to variations in the total number of somites formed, the last somite being always the segment of the genital exit. The Chilopoda, the Protura, and the Collembola are alike in so far as the genital opening in each sex occurs on the last somite, but there is a great discrepancy in the number of somites between the genital segment and the mouth, there being 11 in Collembola, 17 in Protura, 21 to 30 in most Chilopoda, and as many as 175 in the Geophilomorpha. In these opisthogoneate groups new somites are not formed after the genital segment is established; in Hexapoda other than Protura and Collembola one post-genital somite may be added (during embryonic development) in the male, and four in the female. In the progoneate myriapods the seventh postoral somite becomes the genital segment, and an indefinite number of segments is generated in the postgenital region. The genital segment of Chelicerata is always the eighth postoral somite; in Malacostraca it is the tenth in the female and the twelfth in the male, but in both these groups there is a fixed number of postgenital segments.

The recent proposal made by Tillyard (1935) that the genital segment is an identical primitive somite in all the Arthropoda, and that its position in the definitive series of body segments is a matter of whether other somites have been added before or behind it, entirely disregards the evidence that somite formation in the arthropods proceeds always from a generative zone just before the telson. If teloblastic growth is a fundamental principle of development in the Arthropoda, the segment of the genital ducts cannot be an identical somite in all cases, and it is evident, therefore, that the genital outlet segment is not necessarily predetermined as such by morphological heredity.

## EVOLUTION OF THE GENITAL EXIT APPARATUS

The free liberation of the gametes into the surrounding medium, where conjugation takes place as circumstances permit, is the usual mode of propagation with aquatic animals from coelenterates to fishes, though there are various exceptions to the rule. This method of propagation, however, becomes entirely impracticable for terrestrial animals. Hence, animals that live customarily on land either revert to the water at the breeding season, or they develop a genital apparatus for the direct transfer of the spermatozoa from the male into the body of the female. Propagation by sex mating, however, demands a fixed location of the genital orifices at definite points on the body wall in each sex, and the presence of an effective ejaculatory apparatus in the male. It is usually increased in efficiency by the development of a male intromittent organ, a female receptaculum seminis, and various devices for copulation.

All modern Arthropoda, except parthenogenetic and hermaphroditic forms, propagate by sex mating. This fact need not be construed to mean that the ancestors of the arthropods were terrestrial, but, if the mating habit was established by aquatic progenitors, it made the arthropods easily adaptable to life on land. Among aquatic forms, however, the sperm are not in all cases inserted into the genital ducts or a receptaculum of the female. With the Pycnogonida, the Xiphosurida, and many of the Crustacea, though copulation takes place, the eggs are inseminated outside the body of the female at the time of mating, and are then carried by one sex or the other, or deposited at the bottom of the water. In some of the Crustacea packets of sperm are attached to the under surface of the female's body, and fertilization of the eggs takes place later. With the majority of the arthropods, however, the spermatozoa or spermatophores are received into an ectodermal pocket of the female (thelecum, receptaculum seminis, spermatheca) situated near the openings of the oviducts, usually in close proximity to them. The eggs in most such cases are then fertilized as they issue from the ducts. The storage of the sperm in an ectodermal receptacle is thus only a modification of external insemination. In some arthropods, however, the sperm are introduced directly into the oviducts, and fertilization of the eggs may then take place in the ducts or in the ovaries. Finally, there is often present in the female an ectodermal pouch, the bursa genitalis, or genital chamber (bursa copulatrix), which receives the end of the male intromittent organ, and contains the spermathecal and oviducal apertures.

The primary exit ducts of the gonads must be principally mesodermal structures, considering their coelomic origin, but if they have

utilized the primitive coelomic outlets, each should have a small terminal part derived from the ectoderm. The primary gonoducts (fig. 4 A, *Gd*) are the *vasa deferentia* in the male, the *oviductus laterales* in the female. Their external openings are the primary gonopores (*Gprs*). The mesodermal ducts are usually provided with muscular sheaths for the expulsion of the gametes, but with most of the arthropods there has been added to the primary ducts, particularly in the male, a more effective *exit apparatus* formed of evaginations and invaginations of the body wall at the mouths of the ducts, usually accompanied by a special development of associated muscles. These ectodermal parts of the exit system are highly variable, but, on the other hand, they are often very similar in widely separated arthropod groups, in which the gonopores are situated on quite different body segments. Therefore, though it is convenient to employ a uniform system of nomenclature for these parts so far as possible, the use of the same terms in the description of the genital organs of different groups should not be taken to imply anything more than a structural or functional analogy in the parts named alike.

One of the first steps in the development of ectodermal genital accessories may consist merely of the formation of an external papilla bearing the opening of each duct (fig. 4 B, *Pen*). Such structures are usually termed *penes* in the male, whether they are functionally intermittent organs or not, but they may be present also in the female, as in *Xiphosura*. On the other hand, the mouth of each duct may be carried inward at the end of a tubular ectodermal ingrowth (*C*, *Dej*), which usually has a strong muscular sheath, and is termed a *ductus ejaculatorius* in the male, though the term would be quite as appropriate in the female. It is evident that the primary gonopores (*A*, *Gprs*) are now at the inner ends of the ejaculatory ducts (*C*), but to avoid a multiplicity of names the term *gonopore* is applied to the opening of any genital duct, whether primary or secondary. A combination of ejaculatory ducts with external penes is of common occurrence (*D*).

The primitive paired condition of the genital openings and associated structures is retained in some members of most of the arthropod groups, and is characteristic of Xiphosurida, Crustacea, and Diplopoda. In other groups, and in some of the crustaceans and diplopods, an unpaired condition of the terminal parts arises in various ways, and is subject to great modifications, which reach an extreme degree of development in the insects. In the first place, the penis may be a single median organ (fig. 4 E, *Pen*) with two separate openings for the ducts; but in general there is associated with a median penis a single ejaculatory duct (*F*, *Dej*), which receives the two vasa defer-

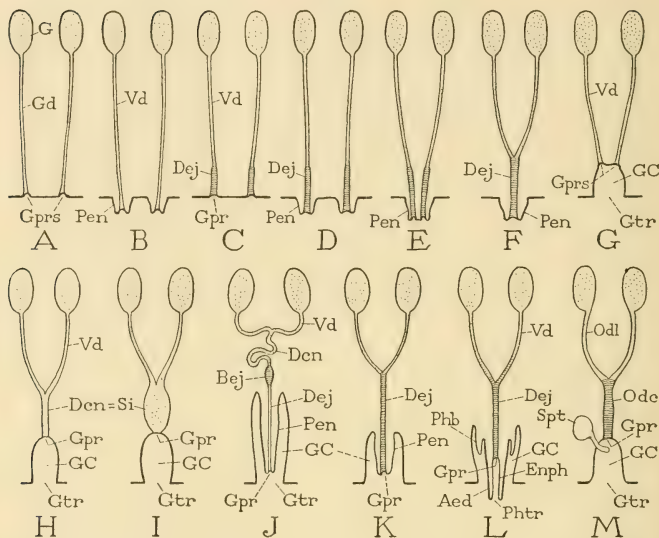


FIG. 4.—Diagrams showing some of the principal variations of the genital ducts and accessory structures.

A, simple condition with gonoducts opening separately through pores of body wall. B, vasa deferentia opening on a pair of penes. C, each vas deferens discharging through an ectodermal ductus ejaculatorius. D, the ejaculatory ducts opening on a pair of penes. E, the ejaculatory ducts opening separately on a single penis. F, a single ejaculatory duct and a single penis. G, the vasa deferentia discharging into a bursa genitalis, or genital chamber (GC). H, the vasa deferentia united distally in a ductus conjunctus (Dcn). I, the ductus conjunctus enlarged to form a sacculus internus (Si), as in many Arachnida. J, a penis evaginated from the genital chamber, traversed by an ectodermal duct from an ejaculatory bulb (Bej), as in Phalangida. K, simple condition in insects, with ejaculatory duct, penis, and genital chamber. L, more complex condition in insects: penis subdivided into phallobase (Phb) and aedeagus (Aed), with ejaculatory duct discharging into an endophallic chamber (Enph); vasa deferentia may be partly replaced by arms of the ejaculatory duct. M, usual structure of genital exit passage of female insects: the common oviduct (Odc) opens into a genital chamber (GC), from which opens the spermatheca (Spt).

Aed, aedeagus; Dcn, ductus conjunctus; Dej, ductus ejaculatorius; Enph, endophallus; G, gonad; GC, genital chamber, or bursa genitalis; Gd, gonoduct; Gprs, gonopore (opening of a genital duct); Gtr, gonotreme (opening of the genital chamber); Odc, oviductus communis; OdL, oviductus lateralis; Pen, penis; Phb, phallobase; Phtr, phallotreme (opening of the endophallus); Si, sacculus internus; Spt, spermatheca; Vd, vas deferens.



entia at its anterior end. The median penis of insects the writer (1935) has designated the *phallus*, but the insect phallus is an intermittent organ, whereas the median penis of most of the other arthropods is not. A median ejaculatory duct is probably in some cases a product of the union of paired ectodermal ducts (a *ductus conjunctus*), and in others an independently developed single invagination (*ductus communis*) at the approximated orifices of the primary ducts.

Another series of modifications in the development of unpaired external genital structures begins with the formation of a wide, open cavity of the ectoderm, into which the primary gonoducts discharge (fig. 4 G, *GC*). The external pouch in this case is the *bursa genitalis*, or *genital chamber*, and may be present in both the male and the female. Its usually large external opening is the *gonotreme* (*Gtr*). The mesodermal ducts (*Vd*) may open separately into the genital chamber (*Gprs*), or their proximal parts may combine to form a *ductus conjunctus* (H, *Dcn*) with a single gonopore (*Gpr*). This condition is common in the Arachnida, where the ductus conjunctus is often enlarged as an inner chamber, *saccus internus* (I, *Si*), of the exit apparatus. An unusual development among the Arachnida occurs in the Phalangida (J). The genital chamber (*GC*) here contains in each sex a large organ evaginated from its inner wall, which serves as a penis in the male (*Pen*) and as an ovipositor in the female. The organ is traversed by a slender ejaculatory duct (*Dej*) beginning with a *bulbus ejaculatorius* (*Bej*), into which opens the ductus conjunctus (*Dcn*) formed by the united vasa deferentia.

The bursa genitalis, or genital chamber, is of common occurrence also in both sexes of the Chilopoda and Hexapoda. In these two groups there is generally present in the male a single median penis, which in its simplest form is merely a conical or tubular outgrowth of the inner wall of the genital chamber (fig. 4 K, *Pen*) traversed by the ejaculatory duct (*Dej*) opening through the gonopore (*Gpr*) at its extremity. The median penis, or *phallus*, of the insects, however, may become a highly complex organ. It is often differentiated into a proximal part, or *phallobase* (L, *Phb*), and a distal *aedeagus* (*Aed*). The gonopore (*Gpr*) commonly becomes concealed within an end chamber, or *endophallus* (*Enph*), and the external opening is then the *phallotreme* (*Phtr*). In female insects the opening of the *oviductus communis* (M, *Odc*), which is the true gonopore (*Gpr*), is usually concealed in a large genital chamber (*GC*), the exposed external opening of which, or *vulva*, is the gonotreme (*Gtr*). The genital chamber contains also the aperture of the spermatheca (*Spt*), and is sometimes narrowed as a tubular *vagina* continuous with the median oviduct.



## THE EXTERNAL GENITALIA

In a wide sense the external genitalia comprise all the secondary sexual characters or modified organs that are concerned with sex mating and egg laying, regardless of their position relative to the opening of the genital ducts. They include copulatory organs, the organ or organs of sperm discharge and intromission in the male, and in the female the seminal receptacle, often a copulatory pouch, and an ovipositor. Because of the variation in the position of the genital apertures, most of the external genital organs have no homology between the several major groups of arthropods, and very different structures may be similarly modified to subserve the same purposes.

The copulatory organs may be defined as structures that serve to hold the two mating individuals together during the insemination of the female or of the eggs. In some cases copulation is effected entirely by the intromittent organ of the male and the receiving pouch of the female; but more commonly the actual copulating, or holding of the female by the male, is performed by the legs or other appendages, which may be particularly modified for the purpose, and there may be developed also special processes of the body specifically adapted for clasping. In nearly all the arthropod groups some of the segmental appendages of the male are more or less altered in structure to serve as clasping organs. In the insects the legs may be used for holding the female and are sometimes modified to this end, but the most important copulatory structures of insects are the appendages of the male genital segment, which are often highly modified and intricately adapted to their function, though there may be present other appendicular, or non-appendicular, structures that have a similar or accessory function. If the female has any special organ of copulation it is usually the pouch that receives the male organ, which in most cases is a genital chamber (*bursa genitalis*) into which the oviduct opens; but the copulatory organ may be the seminal receptacle (*spermatheca*) itself, the orifice of which is sometimes specially adapted for the reception of the apical part of the male intromittent organ.

The intromittent organs of male arthropods include a great variety of structures. Only in rare cases do the paired penes serve for the actual introduction of the sperm into the female receptacles; a direct insertion of the two penes into the corresponding genital apertures of the female, however, is said to take place in certain entomostracan Crustacea, and it is possibly the mode of coition in the Ephemeroptera among the insects. In general, however, where paired penes occur, as

in Xiphosurida, Malacostraca, and Diplopoda, or where in these same groups there may be a single median penis, either the eggs are inseminated outside the body of the female, or the sperm are transferred to the female receptaculum by specially modified appendages (gonopods). In the Malacostraca the intromittent organs are the appendages of the first and second abdominal segments, so modified as to form organs for receiving the sperm or spermatophores from the penes or penis, and for inserting them into the oviducts or sperm receptacles of the female. Similarly in the proterandrious Diplopoda the eighth, or the eighth and ninth, pairs of legs are modified for intromittent purposes, the genital outlets being situated on a pair of penes, or a median penis, on the segment of the second pair of legs. Among the Arachnida the intromittent organs are the chelicerae in Solpugida, the pedipalps in Araneida. The males of opisthandrious Diplopoda are said to use the mandibles for transferring the sperm to the female. A nonappendicular intromittent organ not associated with the genital aperture occurs in the insect order Odonata. This organ is a large, median, penislike structure on the under surface of the second abdominal segment of the male, which receives the sperm from the genital opening on the ninth segment and is the agent of transfer to the female during copulation.

The median penis becomes the functional intromittent organ principally in the Chilopoda and the Hexapoda, though the mating habits of entomostracan Crustacea having a median penis are not well known, and a prominent exception among the arachnids occurs in the Phalangida, in which the sperm are transferred to the female through a large unpaired organ containing the genital exit duct. The penis of the chilopods is never highly developed, and appears to be merely a fold or conical outgrowth of the body wall around the genital aperture. The median penis (phallus) of the insects may be a small simple structure as in the chilopods, but more usually it has a tubular form, and may attain a great complexity of structure. Students of insect morphology have often regarded the insect penis as having some relation to the gonopods of the male genital segment (ninth abdominal), the organ being supposed to be formed by the union of branches or lobes from the bases of these appendages. The ontogenetic development of the insect penis, however, as will be shown in a later part of this paper, does not support this view, and considering that the analogous organs in other groups of arthropods are mere integumental outgrowths, there seems to be no reason for assuming the organ has any other morphological status in the insects.

## II. ONYCHOPHORA

The Onychophora undoubtedly belong to the annelid-arthropod group of animals; their development is typically metameric and the embryonic mesoderm contains a complete series of segmental coelomic sacs. Certain features of their structure definitely separate the Onychophora from the Arthropoda, but, on the other hand, several important anatomical characters common to these two groups would appear to relate the onychophorans more closely to the proarthropods than to the annelids.

The structural disparity between the Onychophora and the Arthropoda is shown particularly in the nervous system and in the body musculature. The longitudinal nerve cords of the Onychophora not only do not form ganglia, but, instead of coming together as in the annelids and arthropods, they move farther apart during their development, and in the adult they lie laterad of a series of dorsoventral muscles on each side of the body that would prevent their median approximation. In the brain, the antennal nerve tracts run dorsal to the optic lobes instead of ventral to them as in the arthropod brain. The onychophoran body musculature consists of a continuous subepidermal muscle layer composed of distinct sets of circular, oblique, and longitudinal fibers, the arrangement of which in no way suggests a possible primitive pattern of arthropod musculature.

The relationship of the Onychophora to the Arthropoda is suggested by the leglike segmental appendages of the latter, though the onychophoran "legs" are little more than well-musculated pouches of the body wall bearing each a pair of claws. It is in the evolution of the mesodermal organs that are shown the most important features common to the Onychophora and Arthropoda. In each group the haemocoel is restored as the permanent body cavity as a result of the reduction or complete dissolution of the coelomic sacs. The nephridia of the Onychophora are coelomoducts, each with a remnant of the corresponding coelomic sac attached to its inner end. The head glands of Crustacea have the same structure as the onychophoran nephridia, suggesting that they have had a common origin with the latter, though they have lost the vibratile cilia still retained in the nephridial canals of the Onychophora. Finally, the reproductive system of the Onychophora is decidedly arthropodan in its structure, since the germaria (equivalent to the "gonads" of Annelida) are enclosed in gonadial sacs derived from the coelomic walls, and the gametes are discharged through gonoducts formed from a pair of coelomic sacs and their outlets. The structure of the nephridial and genital organs in the Onychophora and Arthropoda is, of course, a

necessary result of the general obliteration of the coelomic walls, and therefore might be supposed to be an independent development in each case.

The testes of Onychophora lie dorsally in the posterior part of the body; they are tubular in form (fig. 5 C, D, *Tes*) but vary in length in different species. Each discharges immediately into a saclike semi-

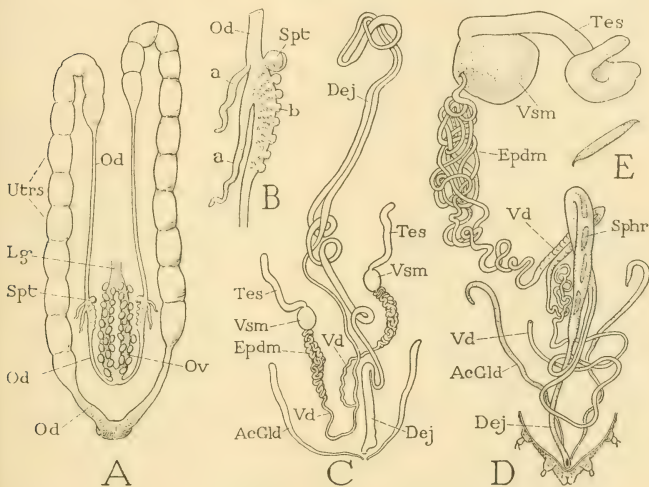


FIG. 5.—Onychophora: internal reproductive organs.

A, *Peripatoides novae-zealandiae*, female organs, dorsal view. B, same, ovarian end of oviduct with spermathecal and other diverticula. C, *Peripatus tholloni*, male organs (from Bouvier, 1905, with parts separated for clearness). D, *Peripatopsis blainvillei*, male organs (from Bouvier, 1902, with accessories omitted). E, same, spermatophore (from Bouvier, 1902).

a, b, diverticula of oviduct; AcGld, accessory genital gland; Dej, ductus ejaculatorius; Epdm, epididymis; Lg, ovarian ligament; Od, oviduct; Ov, ovary; Sphr, spermatophore; Spt, spermatheca; Tes, testis; Utrs, uterus; Vd, vas deferens; Vsm, vesicula seminalis.

nal vesicle (*Vsm*) with muscular walls, within which the spermatozoa are matured. The slender vasa deferentia (*Vd*) proceeding from the vesiculae are much convoluted and the upper part of each usually forms an epididymislike mass of closely entangled coils (*Epdm*). The ductus ejaculatorius (*Dej*) is a long, strongly muscled tube bent upon itself and often looped. The spermatozoa are enclosed in spermatophores formed within the upper part of the ejaculatory duct (D, *Sphr*). The spermatophores vary much in size and form in

different species from small podlike capsules (E) to long tubes or flask-shaped structures. Associated with the genital organs of the male is a pair of tubular accessory glands (C, D, *AcGld*).

The ovaries of the female are a pair of short tubes (fig. 5 A, *Ov*) lying above the alimentary canal near the posterior end of the body. The two organs are united at each end, and are suspended anteriorly by a broad ligament (*Lg*) from the dorsal diaphragm. The growing oocytes are contained individually in follicular diverticula of the ovarian walls, and the mature ova are fertilized within the ovaries or in the oviducts close to them. The oviducts are long tubes looped forward from the united rear ends of the ovaries and then backward to open into a common median invagination of the body wall at the

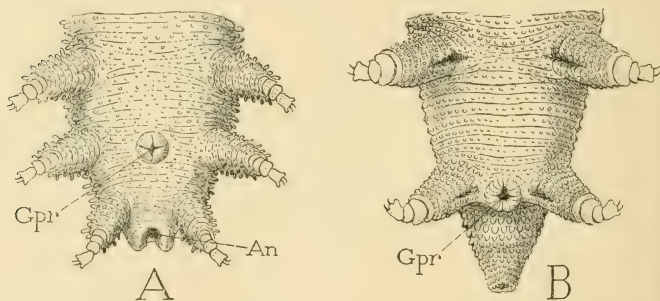


FIG. 6.—Onychophora: position of the genital openings.

A, *Peripatus*, gonopore (*Gpr*) between penultimate pair of legs. B, *Peripatoides novae-zealandiae*, gonopore between last pair of legs, but true terminal pair of legs probably here suppressed.

gonopore (*Od*). In most species each oviduct is provided with a small spermatheca (A, B, *Spt*) in the neighborhood of the ovary, and may have also other tubular or vesicular diverticula (B, *a*, *b*). The majority of the Onychophora are viviparous, and in such forms the embryos develop to maturity in uterine chambers of the oviducts (A, *Utrs*); with oviparous species the relatively large eggs are discharged from the body before development begins. Development is always direct, and the newly born or newly hatched young have the form of the adult.

Both male and female Onychophora have a single external genital opening (fig. 6, *Gpr*), which is located near the posterior end of the body, probably in all cases on the same body region, which is the venter of the penultimate somite before the terminal anal cone. When



all the somites have appendages, therefore, the gonopore lies between the penultimate pair of legs (A); but in some forms the legs of the last somite or of the last two somites are absent, and in such cases the gonopore is either between (B) or behind the last pair of legs present. The opening is usually situated on a small papilla, which may take the form of a short conical or tubular projection serving as a penis or as an ovipositor. Copulation in the Onychophora apparently has not been observed. Males in confinement have been recorded (Sedgwick, 1885) as depositing the spermatophores at random upon the outside of the female's body, but since the spermatozoa are found in the female within the oviducts and the spermathecae it would seem that normally the spermatophores must be transferred from the male directly into the genital opening of the female.

### III. PYCNOGONIDA (PANTOPODA)

The body of a pycnogonid (fig. 7 A) consists principally of the appendage-bearing region composed of seven or eight segments, some of which are united; anteriorly, however, there is a large proboscis (*Prb*) with the mouth at its extremity, and posteriorly a rudimentary, unsegmented abdomen (*Ab*) bearing the anus. The first and second appendages (*Chl*, *Pdp*) evidently correspond with the chelicerae and pedipalps of other Chelicerata. The following appendages are leglike in form and have an ambulatory function, except the slender first pair (*IL*), which are used by the male for carrying the eggs, and which are much reduced or absent in the females of some species. The usual number of legs, including the "ovigerous legs", is five pairs, but in a few genera there are six pairs. The fifth legs are the seventh pair of postoral appendages, and thus correspond with the chilaria of *Xiphosura* (fig. 8 A, *Chi*). The sixth legs, therefore, when present, are represented in the Xiphosurida by the broad plate-like operculum of segment *VIII*, on the posterior surface of which are the genital apertures.

The genital openings of the pycnogonids in each sex are situated ventrally on the second segments of the legs (fig. 4 A, *Gprs*, B, C, *Gpr*). Typically there is a gonopore on each of the ambulatory legs, but the openings may be limited to the last two or three pairs, and in two genera they occur only on the terminal legs. During mating the male grasps the female, either dorsally or ventrally, and the eggs apparently are fertilized externally as they issue from the female. The fertilized egg masses are carried by the male attached to his ovigerous legs.

The segmental duplication of the gonopores in the Pycnogonida might seem to give support to the view that the primitive arthropods



had metamerically repeated gonads with individual segmental outlets. The ovaries and testes, however, which are formed during larval metamorphosis, are said to take first the form of a pair of simple tubes united with each other above the alimentary canal; later they acquire the characteristic branched adult structure by the extension of lateral diverticula into the leg bases above similar diverticula of the alimentary canal. The development of an outlet on each leg, therefore, may be merely the result of the great reduction of the body.

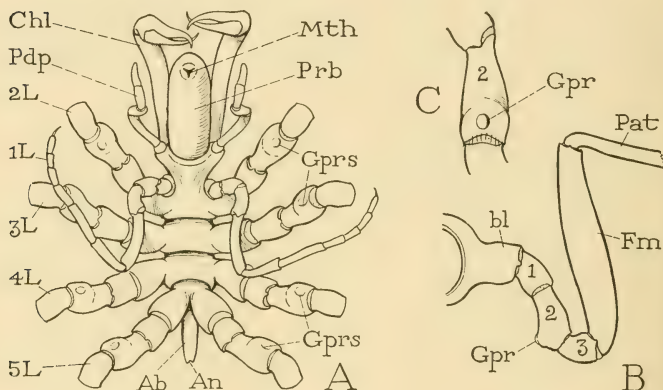


FIG. 7.—Pycnogonida: position of the genital openings.

A, *Chaetonymphon spinosum*, female, ventral view of body and bases of legs, with four pairs of gonopores (*Gprs*) on the second leg segments. B, same, base of leg, anterior view, showing position of gonopore. C, same, mesal view of gonopore.

*bl*, leg-bearing body lobe; *Chl*, chelicera; *Fm*, femur; *Gpr*, *Gprs*, gonopore, gonopores; *1L*, first leg; *2L-5L*, ambulatory legs; *Mth*, mouth; *Pat*, patella; *Pdp*, pedipalp; *Prb*, proboscis; *1, 2, 3*, three small proximal leg segments.

The writer has been unable to find any information on the mode of origin of the genital ducts in the Pycnogonida, but since the segment of the genital openings is not fixed in the arthropods generally there is no reason why a condition of multiple openings might not be a secondary development. It should be observed, furthermore, that the position of the pycnogonid gonopores on the second segments of the legs does not conform with that of the genital apertures in other arthropods having the gonopores on the legs, since in the latter (Crustacea, Diplopoda) the apertures are on the bases of the first leg segments. In any case, the pycnogonids are in no sense primitive arthropods, since they are highly aberrant chelicerates, and have no similarity

to the trilobites. It is important to note, however, that in forms with six pairs of legs the body is divided into prosoma and opisthosoma between segments *VIII* and *IX* as in Xiphosurida, whereas in the other Chelicerata the division is between segments *VI* and *VII*.

#### IV. XIPHOSURIDA

The body of a horseshoe "crab" is distinctly divided into an anterior section and a posterior section, commonly called the *prosoma* and the *opisthosoma* (or cephalothorax and abdomen); but, as will presently be shown, the dividing line between the two parts does not correspond with that separating the two body regions termed prosoma and opisthosoma in the Arachnida, whereas, on the other hand, it is identical with that between the two body regions of Pycnogonida having eight pairs of appendages.

Each section of the xiphosurid body is covered by a broad carapace having the marginal parts widely inflected on the ventral surface of the animal. The opisthosoma is freely movable on the prosoma by a long transverse hinge between its carapace and the prosomal carapace. On the ventral surface (fig. 8 A) are 13 pairs of appendages, including the chelicerae (*Chl*), the pedipalps (*Pdp*), four pairs of legs (*1L-4L*), the chilaria (*Chi*), and 6 pairs of broad platelike structures overlapping each other posteriorly against the under surface of the opisthosoma. The first pair of these lamelliform appendages are united to form a large flat operculum (*Opl*), which mostly covers the following five appendages (*Apds IX-XIII*). On the posterior (dorsal) surface of the operculum are located a pair of small papillae containing the genital apertures in each sex (fig. 9 B, *Pen*). The other opisthosomal appendages bear each a group of lamelliform gills (*D*, *Brn*).

The dividing line between the two parts of the body in *Xiphosura* appears at first sight to lie between segments *VII* and *VIII*, since the chilaria clearly belong to the prosoma and the operculum is associated with the opisthosomal gill plates. A closer inspection, however, shows that the first appendages actually carried by the opisthosoma are the first pair of gill-bearing plates, and that the operculum hangs from a membranous area of the venter that is continuous laterally with the posterior angles of the prosomal carapace. Hence, as shown by Petrunkevitch (1922), the true division between prosoma and opisthosoma in *Xiphosura* lies between the somite of the operculum (segment *VIII*) and that of the first gill-bearing appendages (segment *IX*). The body division in the Xiphosurida, therefore, cor-

responds with that in species of Pycnogonida having eight pairs of appendages, but not with the division between prosoma and opisthosoma in Arachnida, where the two parts of the body are separated between segments *VI* and *VII*. The genital openings, however, are on the same somite, which is segment *VIII*, in both Xiphosurida and Arachnida.

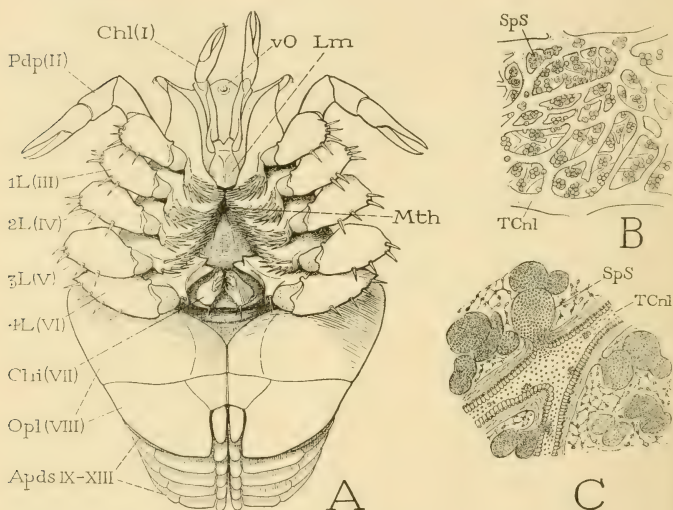


FIG. 8.—Xiphosurida: body appendages and structure of the testes of *Xiphosura polyphemus*.

A, ventral view of body and appendages of young female, with carapace and distal parts of legs removed. B, section of testis, showing testicular canals and sperm sacs (from Benham, 1883). C, part of last, more enlarged (from Benham).

*Apds IX-XIII*, gill-bearing appendages of opisthosoma; *Chi*, chilarium; *Chl*, chelicera; *I-XIII*, postoral somites corresponding with appendages; *1L-4L*, legs; *Lm*, labrum; *Mth*, mouth; *Opl*, operculum; *Pdp*, pedipalp; *SpS*, sperm sac; *TCnl*, testicular canal; *vO*, ventral ocellus.

The male gonads of *Xiphosura polyphemus*, as described by Benham (1883), consist of an intricate network of branching and reuniting testicular canals (fig. 8 B, C, *TCnl*) spread through the entire upper part of the body. The spermatocytes are developed in numerous small follicular diverticula, or sperm sacs (*SpS*), opening from the canals, and the mature spermatozoa are discharged through a pair of short vasa deferentia (fig. 9 B, *I'd*), which open separately on the genital papillae situated on the posterior (dorsal) surface of the base

of the operculum (*Pen*). The organs of the female are essentially like those of the male, and open on a pair of similar papillae.

The operculum (fig. 9 A, B) clearly includes in its composition a pair of appendages similar to the following gill-bearing appendages (C, D), but the median membranous area of its base (B, *V*), on

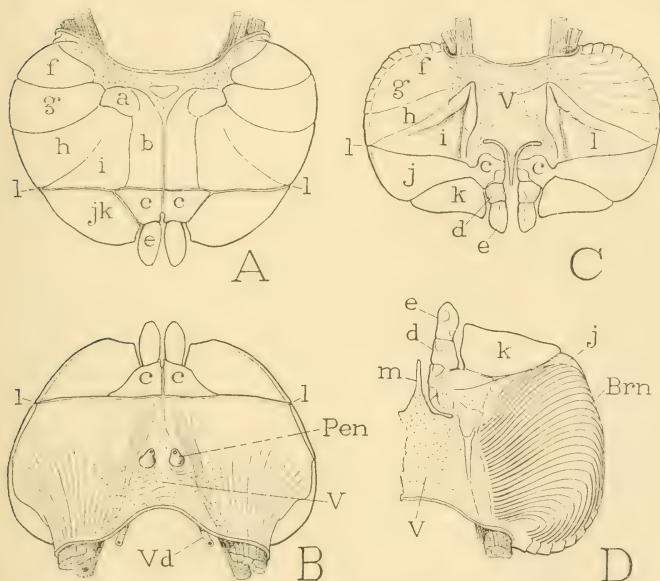


FIG. 9.—Xiphosurida: operculum and first gill-bearing appendages of *Xiphosura polyphemus*, male.

A, anterior (under) surface of operculum. B, posterior (upper) surface of operculum, with penes on median membranous area of base. C, first opisthosomal appendages, anterior (under) surface. D, posterior (upper) surface of right first opisthosomal appendage and median membrane.

*a-l*, subdivisions and sutures of appendages (see text); *Brn*, branchiae; *m*, median tongue of venter; *Pen*, penis; *V*, membranous venter of segment between bases of appendages; *vd*, vas deferens.

which are situated the genital papillae, appears to be a fold of the venter of the opercular segment intercalated between the lateral appendicular elements. In the following segments the median membrane entirely separates the appendages (C, D, *V*) and ends with a free distal process (D, *m*) between them. The genital openings of the Xiphosurida, therefore, are situated, not on the bases of the appendages, but on the venter of the eighth segment, as in the Arachnida.

The xiphosurids copulate during the breeding season, but there is no intromission of the sperm. The eggs are fertilized outside the body of the female and are then usually deposited in sand at the bottom of the water, though the female of *Tachypleus gigas* (*Limulus moluccanus*) is said to carry them attached to the abdominal appendages.

#### V. EURYPTERIDA (GIGANTOSTRACA)

These extinct chelicerates are usually included with the Xiphosurida in the class Merostomata, but they have features characteristic of the Arachnida, and a general appearance that gives them a resemblance to the scorpions.

The body of an eurypterid contains 18 postoral somites (fig. 10 A), and ends with a telson (*Tel*) having the form of a large caudal spine or plate. The two major parts of the body, prosoma and opisthosoma, are separated between segments *VI* and *VII*, as in the Arachnida. The first opisthosomal segment is represented on the dorsal surface of the body by a small tergal plate (*C, VII*), but is not visible on the ventral surface (*A, B*). The first five ventral plates of the opisthosoma (*A, B, VIII-XII*) are said to bear gills on their upper surfaces, and hence probably represent the appendages of these segments united with the median sterna. The first ventral plate (*A, Opl*), since it belongs to segment *VIII*, represents the operculum of *Xiphosura*. It consists of two broad lateral parts separated by a median appendicular process (*oap*) of various forms. This opercular process, by comparison with the abdominal appendages of *Xiphosura* (fig. 9), would appear to be formed, as suggested by Störmer (1934), of the united telopodites of the opercular appendages. It has been supposed to be a genital organ, but this idea seems improbable except in the sense that the process may be a genital accessory of some kind. The genital openings have not been discovered, but it is to be supposed that they are concealed beneath the operculum.

In some of the eurypterids the opisthosoma is subdivided into a preabdomen and a postabdomen (fig. 10 B, C) by a difference in the width of the segments and their apparent mobility. Such forms have a resemblance to the scorpions (D), but it should be observed that the division between the two parts of the opisthosoma occurs between segments *XIV* and *XV* in the scorpions (D), while in the eurypterids (B, C) it is between segments *XIII* and *XIV*. In each group, however, there is the same number of segments in the "tail". Hence, it is possible that the eurypterids have lost one of the segments of the



preabdomen, since the extra segment of the scorpions appears to be in this region of the body. Moreover, the last gill plates of *Xiphosura* and the last lung books of the scorpion are on segment *XIII*, while the last gills of the eurypterids are said to be on

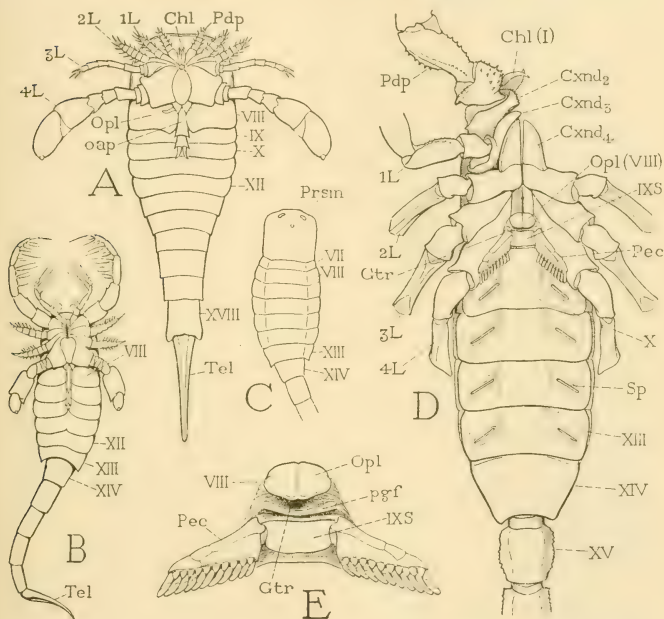


FIG. 10.—Eurypterida and Scorpionida: body segmentation and external genitalia.

A, diagram of an eurypterid, ventral view (from Clarke and Ruedemann, 1912). B, reconstruction of *Mixopterus kioeri* (outline from Störmer, 1934). C, same dorsal view of prosoma and preabdomen. D, body of a scorpion, ventral view. E, ventral parts of genital and postgenital segments of scorpion.

Chl, chelicera; Cxnd, coxal endite; Gtr, gonotreme (opening of genital chamber); 1-XVIII, postoral somites; 1L-4L, legs; oap, opercular appendage; Opl, operculum; Pdp, pedipalp; Pec, pecten; pgf, postgenital fold; Prsm, prosoma; Sp, respiratory orifice; Tel, telson.

segment *XII*. The partial suppression of the first opisthosomal segment is a feature common to Eurypterida and Arachnida. Considering, therefore, the general structure of the eurypterids, so far as it is known, and in particular the arachnid type of their body division into prosoma and opisthosoma, it seems clear that the Eurypterida



are more closely related to the Arachnida than to the Xiphosurida. Aside from the adaptations to terrestrial life by the scorpions, such as the substitution of "lung books" for gills and the correlated suppression of the abdominal appendages or their incorporation in the sternal plates, the principal structural difference between the two groups might be reduced to the elimination of one gill-bearing segment in the eurypterids.

## VI. ARACHNIDA

The number of postoral body segments present in adult or embryonic stages of Arachnida varies from a maximum of 19 in Scorpionida to a minimum of 13 in Araneida (not considering acarid forms in which the body segmentation is obscure). However, since the scorpions are said to have only 18 embryonic postoral neuromeres, it may be true as Petrunkevitch (1922) suggests, that two of the adult segments of the scorpion "tail" represent a single primitive somite, and that the maximum arachnid segmentation, therefore, may include only 18 postoral somites, as in Eurypterida, Malacostraca, and Hexapoda. On the other hand, as already noted, the fact that the last lung books of the scorpions and the last gills of *Xiphosura* are on segment *XIII*, though the last gills of Eurypterida are said to be on segment *XII*, is suggestive that the eurypterids have lost a segment in the gill-bearing region of the body. A terminal spine, poison claw, or flagellum, which is presumably the telson, is not counted in the above enumeration of segments.

The body division into prosoma and opisthosoma in Arachnida is between segments *VI* and *VII*, as in Eurypterida, but segment *VII* is always reduced and is often suppressed, so that the apparent division is usually between segments *VI* and *VIII*. A differentiation of the opisthosoma into a wider anterior preabdomen and a taillike postabdomen is conspicuous in Scorpionida (fig. 10 D), Palpigradida, and Pedipalpida (fig. 11 A). In the first two of these orders the division lies between segments *XIV* and *XV*, but in the third it is between segments *XV* and *XVI*. In no case does the arachnid subdivision of the opisthosoma correspond with the eurypterid division if the latter is actually between segments *XIII* and *XIV*, as it appears to be (fig. 10 B, C), but, as above noted, if it is assumed that the eurypterids have lost a segment in the preabdomen, the segmentation and body division of the eurypterids and scorpions becomes the same.

The Arachnida have a single median genital opening in each sex, which (except in some of the Acarina) always pertains to the second opisthosomal segment, or segment *VIII*, and thus has the same seg-

mental position as the paired gonopores of Xiphosurida; but the position of the opening is variable with respect to the ventral plate of the genital segment, since it is sometimes behind and sometimes before the genital sternum. The arachnid genital aperture is a *gonotreme* (fig. 4 G-J, *Gtr*), inasmuch as it is the immediate opening of an

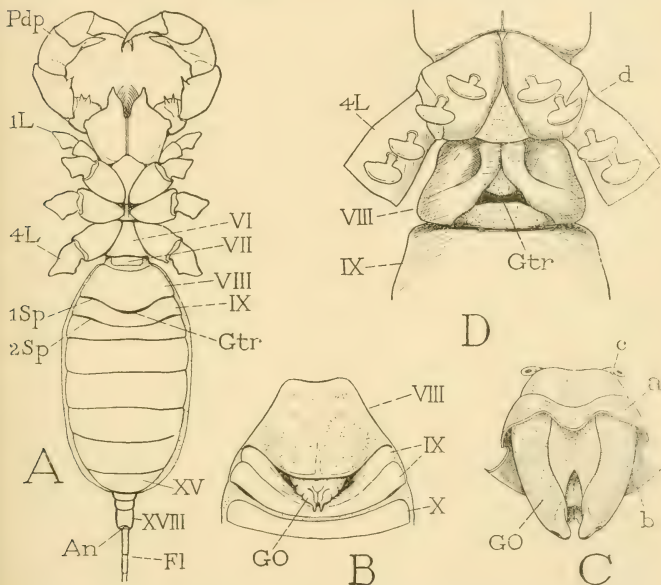


FIG. 11.—Pedipalpida and Solpugida: body segmentation and external genitalia.

A, *Mastigoproctus giganteus*, ventral view. B, *Tarantula palmata* (Amblypygi), base of abdomen of male, ventral surface, with end of genital organ projecting from genital chamber (from Börner, 1904). C, *Tarantula fuscimanus*, male genital organ, dorsal view, exposed by partial removal of walls of genital chamber (from Börner, 1904). D, a solpugid, last prosomal segment and base of opisthosoma with genital opening, ventral view (sex undetermined).

a, b, walls of genital chamber; An, anus; c, genital ducts; d, spatulate appendages of last legs; Fl, flagellum; GO, genital organ; Gtr, gonotreme; 1L-4L, legs; Pdp, pedipalp; Sp, respiratory apertures; VI-XVIII, postoral somites.

ectodermal genital chamber (GC) that contains the true gonopores or gonopore (*Gpr*).

The gonads of the Arachnida lie in the opisthosoma, in some cases above the alimentary canal, in others below it. Each organ in its fundamental structure is a mesodermal tube containing the germinal cells in its epithelial walls, and is continued anteriorly into a cor-

responding gonoduct. Both the gonad and the duct are ensheathed in a muscular coat. The tubular form of the gonad may be retained in the adult, but generally the primary tube becomes branched, producing either a pair of lengthwise tubes, or more commonly a number of lateral diverticula. In some cases the two gonads of opposite sides are united in a single tube or elongate sac, which is either simple or branched. In the Scorpionida mesal branches of the primary gonadial tubes are generally united with each other forming a series of loops, which may join with those from the opposite side, particularly in the female, to produce a composite gonad having the form of a wide-meshed net (see Pavlovsky, 1924, 1924a). The gonad of the net type in the scorpions resembles the reticulate gonad of *Xiphosura* (fig. 8 B) except that the latter has a much finer mesh, but the union of the gonadial branches appears to be independently evolved in the Scorpionida, and is thus no evidence of close relationship between the scorpions and the xiphosurids. In the arachnid ovaries the eggs are developed singly in numerous small follicular diverticula of the ovarian tubes, a feature which the arachnids have in common with Xiphosurida and Onychophora. The embryos of the viviparous scorpions develop either in swellings of the ovarian tubes between the egg follicles or in the follicles themselves.

The gonoducts, regardless of the form of the gonads, are always a single pair of tubes extending usually forward from the ovaries or testes. In both sexes of Scorpionida, in the males of Solpugida and Phalangida, and in the females of Chelonethida, the gonoducts open separately into the genital chamber (fig. 4 G), but in most other cases they unite in a common duct (H) or an inner sac (I) that discharges into the external genital chamber. Since neither the common duct nor the inner chamber is ever found to have a chitinous cuticular lining, the two appear to be structures of mesodermal origin probably formed by the union of the distal parts of the primary mesodermal ducts. The common duct in this case is not strictly equivalent to the usual ectodermal ductus ejaculatorius or the oviductus communis, and is hence here termed a *ductus conjunctus* (fig. 4 H, J, *Dcn*). The inner sac (I, *Si*), which is evidently an enlargement of the ductus conjunctus, is commonly called the "uterus internus" in arachnid anatomy, the name being applied alike in both the female and the male, but since the organ is not functionally a uterus even in the female, it is here termed the *saccus internus* (*Si*). The walls of the inner sac have a strong sheath of muscle fibers, and both the sac and the ducts may be provided with glandular and other kinds of diverticula, including the complex "paraxial organs" of male scorpions described by Pavlovsky (1924).

The external genital chamber, or bursa genitales (fig. 4 G-I, *GC*), commonly known in arachnology as the "uterus externus", is undoubtedly an ectodermal pouch of the body wall since it always has a thick cuticular lining. Into its anterior end open either the paired gonoducts (*G*), or the median ductus conjunctus (*H*) or saccus internus (*I*). Diverticula of the bursal wall form accessory genital glands of various kinds, often of large size, and other structures of unknown function, which in some cases are eversible. In the female a pair of lateral pouches may serve as seminal receptacles. The external opening of the genital chamber, or gonotreme (*Gtr*), as already observed, is always associated with the venter of the second opisthosomal segment, which is segment VIII (figs. 10 D, E, 11 A, D, 13 A, *Gtr*). In the more generalized condition the gonotreme lies behind the sternal plate of the genital segment (figs. 10 E, 11 A, B), but when the genital region is displaced forward between the legs, as in the Phalangida (fig. 13 A), the genital sternum may become reduced or concealed by invagination within the bursa.

A comparison of the external genital structure of the more generalized Arachnida with that of *Xiphosura* shows that the lumen of the genital chamber in the former, into which the gonoducts open, must correspond with the external cavity behind the operculum of the latter, which contains the gonopores. The relation of the arachnid structure to the more primitive condition in *Xiphosura* is particularly evident in the scorpions, where the genital chamber opens behind a small opercular plate or pair of plates (fig. 10 D, E, *Opl*) on the venter of the eighth segment, and the gonoducts open separately into the anterior end of the enclosed cavity. The operculum of *Xiphosura*, as we have seen, clearly includes the appendages of the eighth postoral somite and a median fold of the venter of the same segment (fig. 9 B, *V*), on the posterior surface of which are located the genital papillae (*Pen*). In a truly primitive stage of the Chelicerata (except Pycnogonida), therefore, the paired gonoducts of each sex must have opened on the venter of the eighth postoral segment mesad of the bases of the appendages.

Most of the Arachnida do not have an organ for intromission of the sperm associated directly with the gonotreme. The mating habits of the arachnids are well known only in a few groups, but generally if the male personally inserts the spermatozoa or spermatophores into the sperm receptacle of the female, he uses for this purpose a pair of the body appendages, such as the chelicerae in the Solpugida, or the pedipalps in the Araneida. The female, however, may be inseminated in some indirect manner, as with the Chelonethida. At the time of

mating the male chelonethid attaches to the supporting surface beneath his body a filamentous spermatophore that carries a sperm-containing globule at its upper end; the globule is then taken into the genital opening of the female as the body of the latter passes over it during the mating performance (see Kew, 1912; Chamberlin, 1931). In some of the Pedipalpida and in the Phalangida, however, an exter-

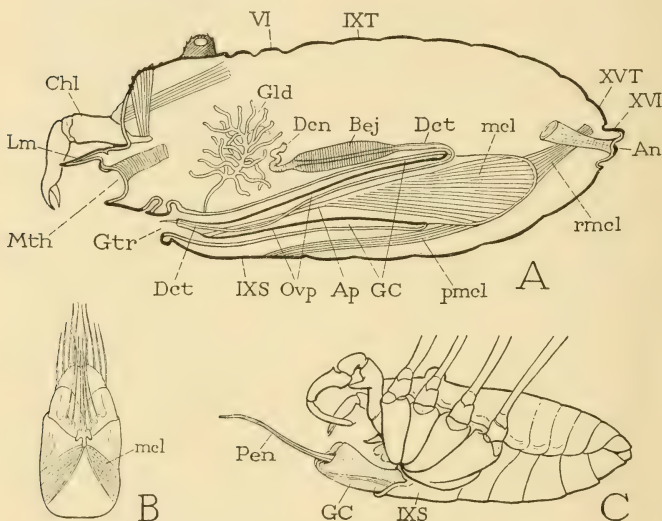


FIG. 12.—Phalangida: male and female genital organs.

A, *Liobunum*, female, diagrammatic longitudinal section of body showing position of retracted external genitalia. B, *Purcellia illustrans* (Cyphophthalmi), genital organ (from Hansen and Sørensen, 1904). C, *Liobunum*, male, genital organ protracted and genital chamber everted.

An, anus; Ap, apodeme; Bej, bulbous ejaculatorius; Chl, chelicera; Dcn, ductus conjunctus; Dct, exit duct of ovipositor; GC, genital chamber; Gld, gland; Gtr, gonotreme; IXS, IXT, sternum and tergum of ninth segment; Lm, labrum; mcl, muscle; Mth, mouth; Ovp, ovipositor; Pen, penis; pmcl, protractor muscle; rmcl, retractor muscle; VI-XVI, postoral somites.

nal genital organ is developed from the walls of the genital chamber, which in male phalangids, at least, undoubtedly serves to convey the sperm to the female. The males of some Acarina, also, have a genital tube which is said to be a true intromittent organ.

The external genital structures of the Pedipalpida are best developed in the genus *Tarantula*, the males of which have a large genital organ (fig. 11 C, GO) ordinarily mostly concealed within the



genital chamber (B). This organ is described by Börner (1902, 1904) as a complex of folds produced from the walls of the genital chamber ("uterus externus"), which enclose a ventral space into which opens the saccus internus ("uterus internus"). The organ is termed a "penis", though only its distal part is entirely free from the genital chamber wall, and its use has not been observed. Börner regards the lateral lobes of the organ as derivatives of the segmental appendages of the genital segment, but of this there appears to be no actual evidence, and, judging from *Xiphosura*, the genital appendages should be merged in the sternal plate of the eighth segment.

Among the Phalangida (Opilionida) the most generalized condition of the external genitalia is preserved in the Cyphophthalmi, where, as shown by Hansen and Sörensen (1904), there is a small sternal plate exposed before the genital opening, and a broad plate behind the latter. If we assume that the true first abdominal sternum is obliterated in the phalangids, as in most other Arachnida, then the pregenital plate must be sternum *VIII*, and the postgenital plate sternum *IX*. In the Phalangidae the anterior part of the venter of the opisthosoma is produced forward into the venter of the prosoma to such an extent that the genital opening comes to lie between the bases of the second pair of legs (fig. 13 A, *Gtr*), and the sternum of the postgenital segment forms a long quadrate plate (*IXS*) between the bases of the third and fourth pairs of legs. Lying before the gonotreme is a transverse fold which may be the sternum of the genital somite, but it appears to belong rather to the segment of the last pair of legs.

The gonotreme of the phalangid *Liobunum* (fig. 13 A) is a wide transverse cleft (*Gtr*) above the anterior margin of the postgenital sternum (*IXS*). It leads into a large sacklike genital chamber with membranous walls (fig. 12 A, *GC*), which in each sex extends far posteriorly in the ventral part of the body. The genital chamber contains a long, tapering, strongly sclerotized genital organ, which is an ovipositor (*Ovp*) in the female and a penis in the male. The organ is a tubular evagination of the posterior wall of the genital chamber, and is transversed by the outlet duct of the gonads (*Dct*). On its base are inserted two pairs of muscles, a long anterior pair (*pmcl*) arising on the posterior angles of the postgenital sternum (*IXS*), and a shorter posterior pair (*rmcl*) arising on the lateral areas of the tergum of the penultimate body segment (*XIT*). The genital organ has the same essential structure in each sex, though there are differences in its size and shape (fig. 13 B, D) to be noted presently. The lateral walls of the genital chamber are strengthened by two long,



thin, flexible sclerotic bands, best developed in the female (D, *b, b*). A pair of large branched glands open into the dorsal wall of the chamber a short distance behind the gonotreme (fig. 12 A, *Gld*).

The female genital organ, or ovipositor, of *Liobunum* is an elongate, continuously sclerotized, flask-shaped structure (fig. 13 D, *Ovp*), widest in its proximal half and tapering forward to its flattened distal end, which bears a small terminal spine (*a*). The expanded basal part of the organ is occupied by two masses of muscle fibers (figs. 12 A, 13 D, *mcl*) that converge distally from the lateral walls to their insertions on a long stalklike apodeme (*Ap*) arising from the ventral wall near the apex of the organ. The base of the ovipositor is deeply emarginate dorsally and ventrally. The dorsal emargination is entered from above by a slender duct (*Dct*) that proceeds from an elongate bulblike structure lying on the dorsal wall of the genital chamber (fig. 12 A, *Bej*), and is itself continuous anteriorly with the median ductus conjunctus (*Dcn*) from the ovaries. The bulb and the duct of the ovipositor are clearly ectodermal structures, since they have a strong cuticular lining. The bulb, *bulbus ejaculatorius* of Rössler (1882), is merely the upper end of the duct surrounded by a thick layer of circular muscle fibers; beyond the bulb the duct becomes an extremely fine cuticular canal without a muscle sheath, traversing the ovipositor to the base of the terminal spine, where it appears to open on the under surface of the latter. In some of the phalangids one or more pairs of small pouches diverge from the outlet duct just behind its opening; these pouches are said to be the sperm receptacles, but they were not observed in the species here described.

The genital organ of the male phalangid (fig. 13 B, *Pen*) has the same general structure as the ovipositor of the female, but in *Liobunum* it is much slenderer than the ovipositor, and in two species examined its distal part is decurved or hooked (figs. 12 C, 13 C, *Pen*). In the specimen shown at C of figure 12 the penis is exerted by a complete evagination of the walls of the genital chamber (*GC*). The initial act of protraction, it would seem, must be caused by a contraction of the long anterior muscles of the penis (fig. 13 B, *pmcl*), but in the fully exerted condition these muscles extend anteriorly to the base of the penis from their origins on the postgenital sternum. It is evident, therefore, that the final stage of protraction results from a general compression of the abdomen that everts the genital chamber. Retraction then must be brought about by the contraction of the reversed anterior muscles acting at first in cooperation with the greatly stretched posterior muscles (*pmcl*), which finally alone complete the process.

The morphology of the external genitalia of the phalangids has not been determined from embryological studies, but there can be no doubt that the cuticular parts, including the genital chamber, the genital organ, the duct of the latter and its bulb, are all derived from the ectodermal genital chamber ("uterus externus") of other arachnids

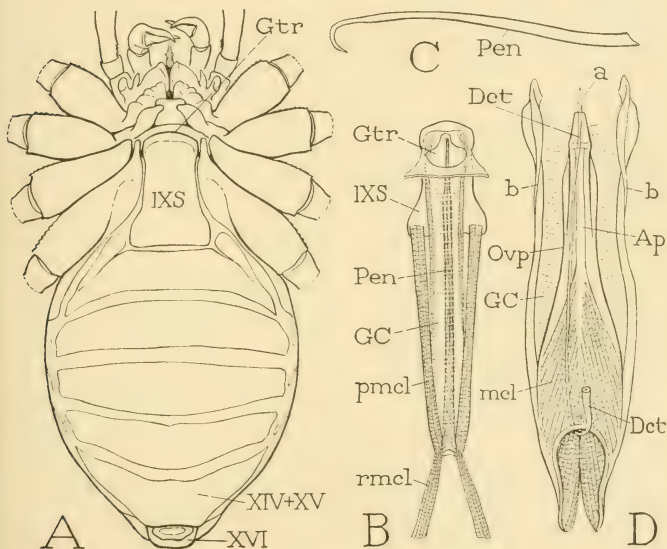


FIG. 13.—Phalangida: body segmentation and genital organs of *Liobunum*.

A, ventral surface of body and appendage bases of a male, showing anterior position of gonotreme (*Gtr*). B, genital organ of male (penis) retracted in genital chamber, dorsal view. C, penis, lateral view. D, genital organ of female (ovipositor) retracted in genital chamber, dorsal view.

*a*, apical point of ovipositor; *Ap*, apodeme; *b*, *b*, lateral sclerites in wall of genital chamber; *Dct*, exit duct of ovipositor; *GC*, genital chamber; *IXS*, sternum of ninth segment; *mcl*, muscle; *Ovp*, ovipositor; *pmcl*, protractor muscle of penis; *rmcl*, retractor muscle; *Pen*, penis; *XIV-XVI*, posterior somites.

(compare I and J of fig. 4). The inner duct (*Dcn*) opening into the bulb from the gonads is a mesodermal ductus conjunctus ("uterus internus"). The muscular bulb and the exit canal constitute an ejaculatory apparatus comparable with the male ductus ejaculatorius (K, *Dej*) or with the female oviductus communis (M, *Odc*) of other arthropods. In most of the Phalangida the genital organ (penis or ovipositor) has a closely ringed structure, and ends in two small

lobes; in some forms (fig. 12 B) it is much shorter than in the Phalangidae.

During mating of the phalangids, according to Henking (1888), the male and female stand face to face, and the male thrusts the penis into the genital opening of the female, its tip apparently entering the aperture of the ovipositor, since there is no other approach to the seminal receptacles. When the eggs are discharged they must traverse the excessively slender duct of the ovipositor; Henking records observations on *Liobunum hemisphaericum* in which he followed the transit of the eggs through the duct and saw their exit from its distal end. Since the duct has no muscular sheath, the eggs must be propelled through it, as noted by Rössler (1882), by the action of the bulbus ejaculatorius, which thus has a corresponding function in both the male and the female. The eggs of *Liobunum* are deposited in the ground.

#### VII. CRUSTACEA

The crustaceans, by comparison with the progoneate arachnids and diplopods or with the opisthogoneate chilopods and hexapods, might be said to be "mesogoneate", inasmuch as the genital openings are on the intermediate part of the body. However, if the numerical position of the segments is considered, the genital segment of some of the many-segmented branchiopods may be as far behind the mouth as that of the chilopods, and considerably to the rear of the genital segments of insects. The segmental position of the gonopores is highly variable in the Entomostraca, but in this group the apertures are always on corresponding segments in the two sexes; in the Malacostraca the genital openings are fixed with specific segments, but they are always on different segments in the male and the female.

To enumerate the postoral trunk segments of the Crustacea in conformity with the enumeration followed in the Chelicerata, we must begin with the somite of the second antennae, which morphologically corresponds with that of the chelicerae.

The gonoducts of the Entomostraca usually open separately to the exterior; in some cases the gonopores are on the limb-bearing thoracic region of the body, but more generally they occur on the abdomen. Intramittent organs are present in some groups, as in Branchiopoda and Ostracoda, the males of which may have a pair of penes, or a single penis through which both vasa deferentia discharge. Examples of the paired type of organ are shown here in two branchiopod species, *Branchipus serratus* (fig. 14 A, B) and *Polyartemia hazeni* (C). The two penes of the first species are short, thick papillae (A, *Pen*) projecting ventrally from the under surface of the second

abdominal segment (somite *XXVII*), but provided with muscles arising in both the second and the first segment. Each penis is armed distally with a hook (B) mesad of which is the gonopore. In *Polyartemia hazeni* the penes (C, *Pen*) are long tubular organs projecting posteriorly from the under surface of the first and second abdominal segments, which in this form are somites *XXI* and *XXII*. The branchiopods, except in cases of parthenogenesis, propagate by sex

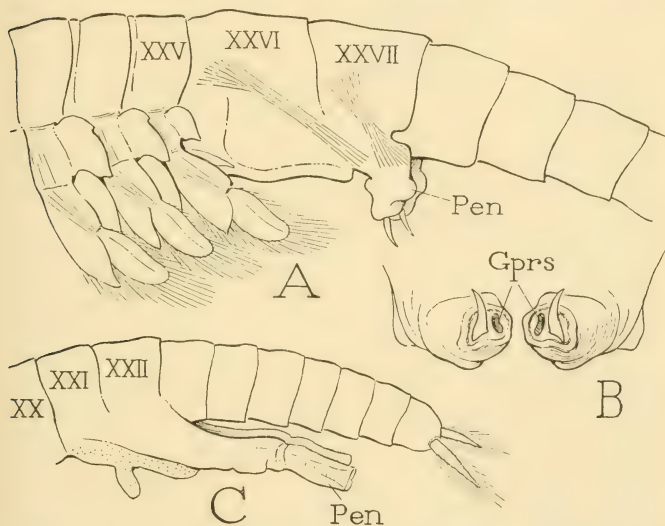


FIG. 14.—Crustacea—Branchiopoda—Anostraca: showing variable position of penes.

A, *Branchipus serratus*, with penes (*Pen*) arising on somite *XXVII*. B, same, end view of penes and gonopores (*Gprs*). C, *Polyartemia hazeni*, with penes on somite *XXII*.

mating, and the spermatozoa are said to be discharged by the male directly into the genital openings of the female; few observations, however, have been made on the exact manner of copulation and intromission.

The Malacostraca have a highly standardized body segmentation, there being, with few exceptions, 18 somites between the mouth and the telson. The trunk is consistently differentiated between segments *XII* and *XIII* into a cephalothoracic region and an abdomen; but the distinction between head and thorax is often somewhat con-

ventional, and when there is a well-marked anatomical separation the boundary is not the same in all cases. Carcinologists usually define the "thorax" as the body region composed of the eight segments between the second maxillary somite (*IV*) and the first abdominal somite (*XIII*), but in some cases the head includes the first of these segments. The abdomen contains six somites and the telson, except in one order, the Leptostraca, in which there are seven abdominal somites. The genital openings of the female are situated always on the sixth thoracic segment (somite *X*), those of the male on the eighth (somite *XII*). In some cases the gonoducts of the male have a single median opening. The female generally is provided with a sperm receptacle, which may be a median pouch of the ventral integument of the thorax, or paired sacs at the ends of the oviducts.

The gonads of the Malacostraca are tubular or sac-shaped organs, sometimes lobed or branched, lying in the dorsal part of the thorax and abdomen, or restricted to the thorax (figs. 15 G, 16 C, 17 C, 18 E). In the decapods the gonads of opposite sides are generally more or less united (figs. 17 C, 18 E). The germinal cells usually occupy one wall of the gonad, from which the oocytes or spermatocytes are proliferated into the lumen (fig. 15 E); the cells of the opposite wall (*NrCls*) may have a nutritive function. In *Anaspides*, as described by Smith (1909), the mesal walls of the ovaries are produced into long series of diverticula, in the apices of which are located the germinal cells, the organs thus resembling the ovaries of insects. The gonoducts are either straight or coiled, and generally open directly to the exterior, but in the Brachyura the oviducts end in large ectodermal sperm receptacles (fig. 18 H, *Spt*).

The gonopores of male Malacostraca are located typically on or close to the mesal surfaces of the coxopodites of the last pereopods (thoracic appendages), though they may lie on the sternal surface between the appendages (figs. 15 D, 16 A, *Gprs*). Usually each aperture is situated on the extremity of a small papilla or tubular outgrowth of the integument (figs. 16 B, 18 D, *Pen*), called a penis though it is not the actual intromittent organ. In some cases there is a single median penis arising from the venter of the eighth thoracic segment (fig. 16 D, *Pen*), which contains a common outlet duct receiving the two lateral gonoducts at its base. If direct internal insemination of the female from the penes, or penis, of the male takes place in any of the Malacostraca it is of rare occurrence, and has not been observed. With the majority of the Malacostraca the sperm (or spermatophores) are placed by the male in the oviducts or in a sperm receptaculum of the female, but the organs that accomplish the intro-



mission are usually modified parts of the first, or the first and the second, pleopods (abdominal appendages). In some cases, however, the spermatophores are merely attached to the under surface of the body of the female. Fertilization of the eggs takes place either within the oviducts, or in a brood pouch on the under surface of the female's body. A few examples of the external genitalia of the Malacostraca

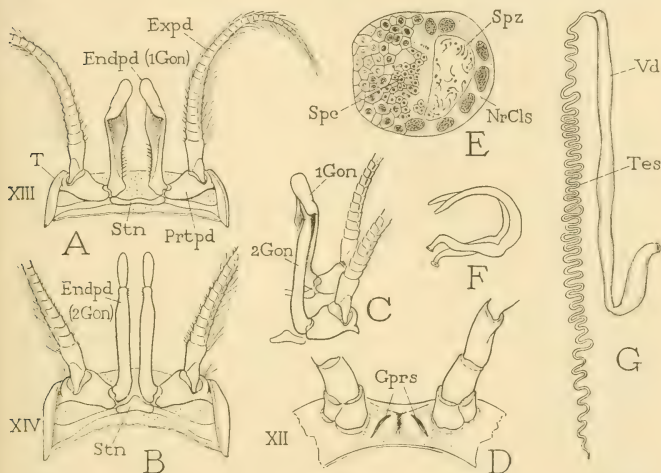


FIG. 15.—Crustacea—Malacostraca—Syncarida: male genitalia of *Anaspides tasmaniae*.

A, B, appendages of first and second abdominal segments, ventral view, showing mesal processes, or gonapophyses (probably the endopodites), that compose the intromittent organs. C, left gonopods, posterior (under) view, showing functional relation of gonapophyses. D, ventral surface of last thoracic segment, with gonopores. E, cross-section of testis. F, spermatophores. G, testis and vas deferens. (E, F, G from Smith, 1909.)

*Endpd*, endopodite; *Expd*, exopodite; *1Gon*, *2Gon*, first and second gonapophyses (probably endopodites); *Gprs*, gonopores; *NrCls*, nutritive cells of testis; *Prtpd*, protopodite; *Spe*, spermatocytes; *Spz*, spermatozoa; *Stn*, sternum; *T*, tergum; *Tes*, testis; *Vd*, vas deferens; *XII*, *XIII*, *XIV*, twelfth, thirteenth and fourteenth postoral somites.

will suffice to illustrate the general structure and variations of the organs in this group.

The typical structure of the external genital organs of male Malacostraca is well shown in the Anaspidacea. In *Anaspides tasmaniae* the male gonopores are two oblique slits on the venter of the eighth thoracic segment (fig. 15 D, *Gprs*) situated on oval elevations between the bases of the last pair of legs. The functional intromittent organs



are composed of two pairs of long processes arising from the inner ends of the basal segments of the first and second pleopods, which are, therefore, probably the endopodites of these appendages (A, B, *Endpd*). The genital processes, or gonapophyses, of the first pair (A) are expanded distally and hollowed on their inner surfaces; those of the second pair (B) are cylindrical, and their distal ends fit snugly into the concavities of the first pair (C). By means of these organs the male during mating inserts a pair of large, horseshoe-shaped spermatophores (F) into a two-branched receptacular pouch opening on the venter of the last thoracic segment of the female. The spermatophores are probably taken from the gonopores of the male into the cavities of the first gonapophyses, and forced from the latter by the second gonapophyses. Within the receptacular pouches of the female the spermatozoa are discharged from the spermatophores, and the latter are then rejected. Since there is evidence that fertilization of the eggs takes place in the oviducts, it is supposed that the spermatozoa are transferred into the openings of the latter on the sixth thoracic segment by means of setigerous lobes, present only in the female, on the inner surfaces of the coxopodites of the last three pairs of thoracic legs. The fertilized eggs are said by Smith (1909) to be deposited singly "under stones and among the roots of water plants" (his figure shows them on the branches of a liverwort).

The Isopoda generally have two separate genital exit ducts, which in the male open either by simple apertures (fig. 16 A, *Gprs*) or through a pair of small penes on the sternum of the last thoracic segment. In the Oniscoidea, however, which include the ordinary terrestrial isopods, there is present usually a single median penis (C, D, *Pen*), and the gonoducts unite at its base in a common exit tube. The median penis may be displaced posteriorly so that it arises from the membrane behind the last thoracic sternum, with its base between the appendages of the first abdominal segment (D, *Pen*). The intromittent organs of Isopoda, when present, are formed as in Anaspidacea of the inner arms, or endopodites, of the first and second pairs of abdominal appendages (D, E, *Endpd*). By means of these structures masses of spermatozoa that issue from the gonopores are inserted into the genital openings of the female. The terminal parts of the oviducts in some species of isopods are enlarged to serve as sperm receptacula, and the eggs are fertilized in the ducts. After mating, the female moults and in most species acquires a brood pouch (marsupium) on the under surface of the body, into which the fertilized eggs are discharged, and within which they are carried until the young hatch. The brood pouch is formed typically by broad

overlapping plates (oostegites) that grow over the thoracic venter from the bases of the legs, but in some species it is formed by anterior and posterior folds of the ventral integument, and in others by an invagination or a series of sacklike ingrowths of the membranous ventral wall of the thorax. In one genus, *Paragnathia*, the young are said to develop in the ovaries, which serve as uteri.

The Amphipoda are provided with a pair of small penes, but they have no organs of sperm intromission; the eggs are fertilized outside

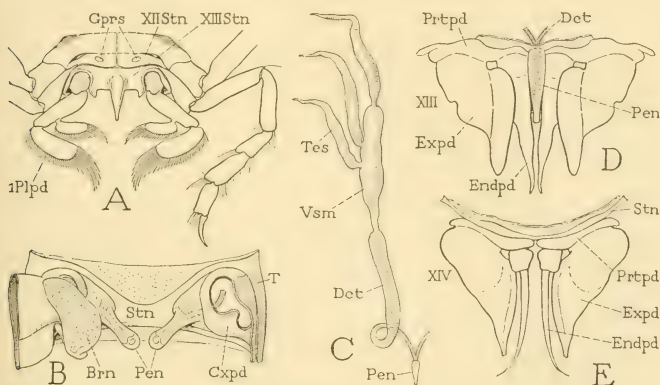


FIG. 16.—Crustacea—Malacostraca—Peracarida: male genitalia of Isopoda and Amphipoda.

A, *Serolis* (isopod), ventral view of last thoracic and first abdominal segments, showing gonopores on sternum of somite XII. B, *Gammarus locusta* (amphipod), ventral view of last thoracic segment, showing penes arising at bases of coxopodites. C, *Porcellio laevis* (isopod), testis and exit duct of one side, and median penis. D, same, penis and first pleopods, ventral view. E, same, second pleopods.

Brn, branchia; Cxp, coxopodite; Dct, genital exit duct; Endpd, endopodite; Expd, exopodite; Gprs, gonopores; Pen, penis; Prtpd, protopodite; Stn, sternum; T, tergum; Tes, testis; Vsm, vesicula seminalis; XIIStn, sternum of male genital segment; XIIIStn, sternum of first abdominal segment.

the body of the female. The penes, as illustrated in *Gammarus locusta* (fig. 16 B, Pen), are a pair of short cylindrical processes arising from membranous areas between the lateral arms of the last thoracic sternum and the bases of the coxopodites. During mating the male attaches himself to the back of the female and remains in this position until the female moults; then immediately the male curves his body under that of the female and attaches small masses of sperm to the body wall of the latter in the neighborhood of the oviducal apertures. The eggs, later extruded, are fertilized in the brood pouch beneath

the body. It is interesting to observe that in the Amphipoda and Isopoda insemination of the female precedes or follows a moult by the latter according as the spermatozoa are stored on or in a part of the body not involved by the moulting process, or in a part subject to removal at ecdysis. Insemination *before* the moult allows the development in the female of special ectodermal structures, such as the oostegites or brood pockets, necessary after the eggs are fertilized.

The Decapoda vary somewhat in their mating habits, but the spermatozoa are enclosed in spermatophores, which either are attached to the external integument of the female, or are inserted into an integumental pocket (*thelycum*, *annulus ventralis*) or into a pair of ectodermal spermathecae associated with the oviducal openings. Insemination of the female, therefore, takes place immediately *after* a moult to insure against premature loss of the sperm.

The external genitalia of male decapods include a pair of penes arising from the mesal surfaces of the coxopodites of the last pereopods, and the modified first and second pleopods, which are the active intromittent organs. The genital structures retain more of the generalized form in the Macrura than in the Brachyura. In *Cambarus virilis* the penes are small membranous lobes projecting mesally from the bases of the last pereopods (fig. 17 A, *Pen*), with the gonopores on their posterior surfaces. The sternum of the genital segment (*Stn*) presents a deep concavity between the coxopodites, which is continued forward on the next two segments, forming a ventral channel of the thorax in which are lodged the anterior ends of the gonopods. The first pair of gonopods are long, rigid appendages (B, D) projecting anteriorly in the thoracic channel as far as the bases of the second pereopods. The shaft of each of these appendages tapers to a slender distal process (*a*), but from its under surface there arises mesally a large lobe that splits into two proximal processes (D, *b*, *c*), the outer one of which (*b*) has a groove on its upper surface that leads into a deep cavity at the base of the lobe. The second gonopods (E) have more nearly the structure of the unmodified pleopods of the following segments. Each is a biramous appendage with the two arms (*Expd*, *Endpd*) supported on a two-segmented basal stalk (*Cxpd*, *ITr*). The larger endopodite bears a mesal lobe (*d*) at the end of its long first segment, which, when the appendage is turned forward beneath the corresponding first gonopod, clasps the latter at the base of its mesal lobe. The structure of the crayfish gonopods and the manner in which the appendages perform their function of sperm intromission during copulation are minutely described for *Cambarus affinis* by Andrews (1911). The spermatozoa are received from the

penes into the grooves of the mesal lobes and the pockets at their bases on the first gonopods, and are discharged into a receptacular pouch (annulus ventralis) on the venter of the female between the sterna

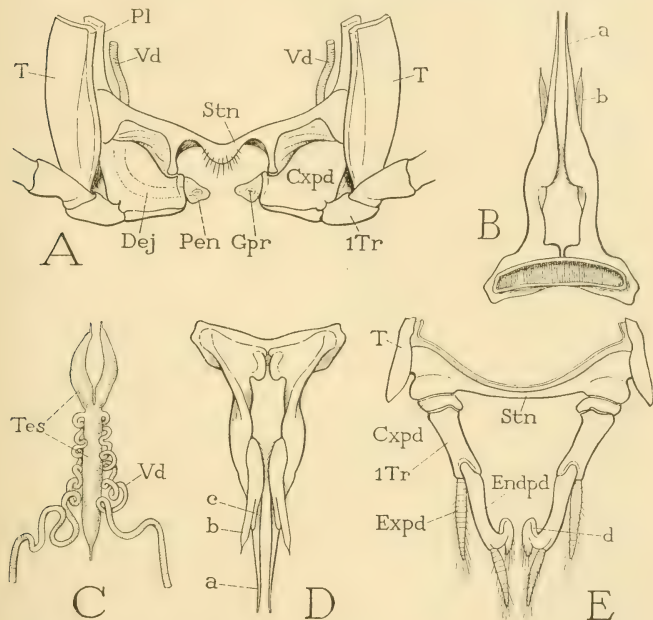


FIG. 17.—Crustacea—Malacostraca—Eucarida: male genitalia of a crayfish, *Cambarus virilis*.

A, posterior view of lower part of last thoracic segment, showing small penes projecting mesally from coxopodites. B, first gonopods projecting forward, anterior (upper) surface. C, testes and vasa deferentia, dorsal view. D, first gonopods (normally projecting forward in ventral channel of thorax), posterior (under) surface. E, second gonopods, posterior (under) surface.

a, distal shaft of first gonopod; b, c, outer and inner branches of ventral lobe of first gonopod; Cxp, coxopodite; d, distal lobe of second gonopod; Dej, ductus ejaculatorius; Endpd, endopodite; Expd, exopodite; Gpr, gonopore; Pen, penis; Pl, pleuron; Stn, sternum; T, tergum; Tes, testis; 1Tr, first trochanter (basipodite); Vd, vas deferens.

of the seventh and eighth thoracic segments. (See also Andrews, 1906.)

The crabs (Brachyura) differ from most of the other decapods in that the female has a pair of large pouchlike sperm receptacles

formed as invaginations of the body wall at the gonopores on the bases of the third pereopods, into which open the short oviducts (fig. 18 H, *Spt*). Inasmuch as the sperm containers are ectodermal structures, insemination takes place just *after* a moult of the female. The paired intromittent apparatus of the male crabs is a complex structure composed of the penes of the last thoracic segment, and the greatly modified first and second pleopods of the abdomen. Both sets of organs are ordinarily concealed in a deep median depression on the under surface of the thorax covered by the T-shaped abdomen when the latter is turned forward in its usual position.

In the blue crab, *Callinectes sapidus*, the principal member of each composite intromittent organ is the first pleopod (first gonopod). This appendage consists of a large flat coxopodite (fig. 18 B, *Cxpd*) projecting laterally from the small triangular sternum of its segment, and of a long tapering telopodite, or "flagellum", with an enlarged base. The thick base of the flagellum (*b*) turns mesally from the end of the coxopodite (A, B), and the slender, tapering distal part (*a*) extends anteriorly, overlapping its mate from the opposite side (B) in the ventral groove of the thorax above the flexed abdomen. The walls of the bulblike base of the flagellum are partly membranous (B, D, *mb*), and the posterior margin of the bulb is cleft by a deep groove that expands inwardly as a large internal cavity; the enlarged ends of the groove form a proximal foramen on the anterior surface of the bulb (D, *c*) and a distal foramen on the posterior surface (B, *d*). The groove, however, is continued from the lower lip of the distal foramen along the entire length of the slender distal part of the flagellum (B, *gr*), forming within the latter a tubular canal continuous with the cavity of the base and opening mesally near the tip. The second gonopod (C) resembles the first in general form, but it is much smaller, and has a small middle segment (*Bspd*) interpolated between the base of the flagellum and the coxopodite; the flagellum (*e*) is a short curved arm no longer than the bulbular base of the first flagellum. The penes of the crab arise from the mesal ends of the coxopodites of the last pereopods. Each is a long flexible tube (D, *Pen*) traversed by the gonoduct, which opens at its extremity.

The component elements of the genital complex of the crab are intimately associated with one another, and constitute an apparatus for conveying the spermatozoa from the male gonoducts into the seminal receptacles of the female. In the normal condition the penis of each composite organ lies mostly within the cavity of the bulbular base of first flagellum, which it enters by the anterior proximal foramen of the latter (fig. 18 A, *Pen*); the end of the second flagellum



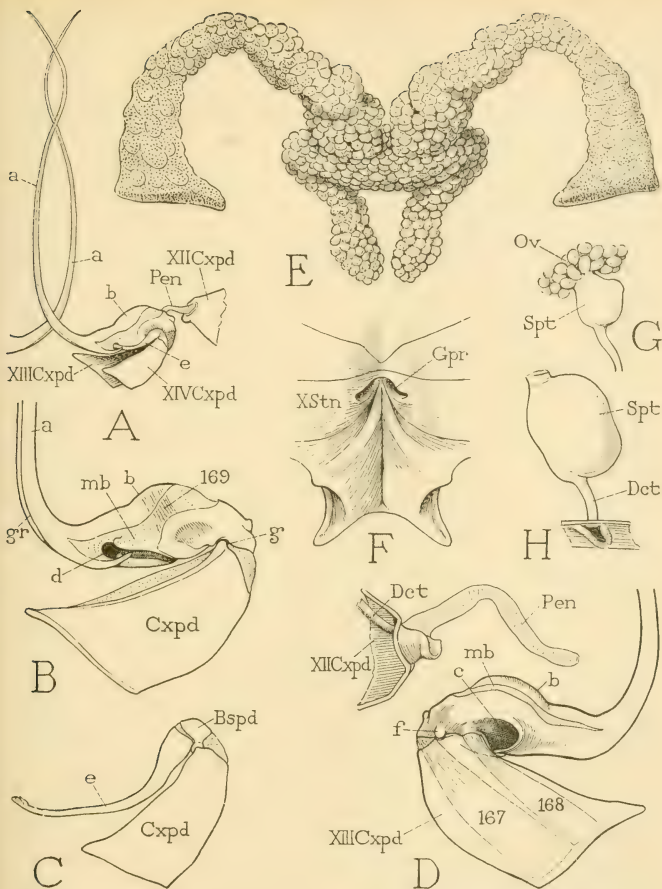


FIG. 18.—Crustacea—Malacostraca—Eucarida: male and female genitalia of a crab, *Callinectes sapidus*.

A, the intramittent apparatus, including on each side the penis and the modified first and second pleopods (gonopods), ventral view. B, base of left first gonopod, posterior (under) surface. C, left second gonopod, posterior (under) surface. D, left penis and base of left first gonopod, anterior (upper) surface. E, ovary, dorsal view. F, gonopores of female on tenth (third thoracic) sternum. G, spermatheca of a young hard-shell female. H, spermatheca of a soft-shell female probably ready for insemination.

a, distal shaft of first gonopod; b, bulblike base of telopodite of first gonopod; Bspd, basipodite; c, anterior proximal foramen of first gonopod; Cxpd, coxopodite; d, posterior distal foramen of first gonopod; Dct, spermathecal duct; e, distal arm of second gonopod; f, g, anterior and posterior articulations of telopodite on coxopodite; Gpr, gonopore; gr, groove of first gonopod; mb, membrane; Ov, ovary; Pen, penis; Spt, spermatheca; XStn, sternum of genital segment of female; XII Cxpd, XIII Cxpd, XIV Cxpd, coxopodites of last pereopods and of first and second pleopods (gonopods); 167, 168, coxal muscles of telopodite; 169, compressor muscle of bulb of first gonopod.



(*c*) similarly enters the posterior distal foramen of the bulb. The second flagellum thus would appear to act as a plunger for driving the sperm through the channel of the first. A strong transverse muscle (B, 169) crosses the middle of the bulb and evidently acts as a compressor of the latter.

The mating habits of the blue crab have been described by Hay (1905) and by Churchill (1921). During the breeding season the male crabs appear to be able to recognize females in a premoulting condition. When a male encounters such a female he seizes her by the back with his second, third, and fourth pereopods, leaving the chelae free for feeding, and the last pereopods (swimming legs) free for swimming. In this position the two crabs swim about for a day or so; but as soon as the female is about to moult, the male releases her on the bottom of the water and stands guard until the shell is cast. The female then turns ventral side up and extends the abdomen, whereupon the male grasps her again, and insemination now takes place while the female is in the soft condition following the moult. The eggs are later fertilized as they are discharged through the seminal receptacles, and are carried in a mass attached to the pleopods of the female until they hatch the following spring.

#### VIII. MYRIAPODA PROGONEATA

The progoneate myriapods include the Symphyla, the Pauropoda, and the Diplopoda. These forms evidently constitute a natural arthropod group characterized by having the genital apertures in both sexes situated on the third postcephalic segment, which segment most probably is the seventh postoral somite. To enumerate the postoral somites in the progoneate myriapods, however, it is necessary to take a somewhat arbitrary view concerning the segmentation of the head and the anterior body region, since the literature on the subject is full of conflicting opinions and different interpretations of the observed facts.

If we start with the Symphyla as a basis for interpreting the progoneate segmentation, the matter is relatively simple, for here the gnathal region of the head supports a pair of mandibles and two distinct pairs of maxillary appendages, and the first postcephalic segment carries a pair of legs. Though postantennal appendages (second antennae) have not been discovered in any of the progoneate myriapods, Robinson (1907) reports the presence of a pair of "second antennal" ganglia in the embryo of a diplopod. It is entirely reasonable to assume, therefore, that the symphyliid head contains four postoral segments representing the second antennal, mandibular, and two maxillary somites of the Crustacea, or the corresponding somites

of Chilopoda and Hexapoda. There can be no question as to the identity of the first body segment in the Symphyla, since, though reduced, it bears a pair of legs. These first legs are small and lack one of the distal segments present in the other legs. Behind the bases of the third pair of legs is situated in each sex the median genital opening, which evidently belongs to the third body segment, though it may invade the venter of the following segment. If, therefore, we count the absent second antennal somite as segment *I*, the genital opening in Symphyla is on segment *VII*, which is the third body segment.

In the Pauropoda and Diplopoda a direct determination of the gnathal and postcephalic segmentation becomes impossible by reason of the facts that in the adult there is only one appendage in the maxillary region of the head, and the first apparent body segment is reduced and lacks appendages. As above pointed out, the evidence deduced from developmental studies is conflicting and inconclusive. By comparison with Symphyla, however, the genital segment of the pauropods and diplopods should be segment *III*, since there is no evidence of variability in the position of the genital outlets in any of the progoneate myriapods. The male exit ducts of the Pauropoda open on a pair of small penes situated at the bases of the second pair of fully developed legs; the first legs, if present, are rudimentary and arise from an apparent neck region, which latter, therefore, must be regarded as the reduced first body segment. The single female outlet duct opens by a median aperture between the bases of the legs on the same segment as in the male. (See Silvestri, 1902; Attems, 1926.)

The Diplopoda have a distinct "neck segment" intervening between the head and the first leg-bearing segment of the body, which typically contains a large dorsal plate, the *collum*, and a small ventral plate, but apparently has no appendages. In the adult there is only one postmandibular appendage on the head, the *gnathochilarium*, which appears to have a composite structure. The first three body segments following the neck segment have each only one pair of legs, and the genital apertures are always on the segment of the second pair. In most of the diplopods (the Proterandria) the eighth or the eighth and ninth pairs of legs (those of the third "double segment") are modified in structure to serve as intromittent organs, and are termed the *gonopods*.

The dispute on the question of diplopod segmentation concerns the number of postoral somites in the head, the nature and composition of the gnathochilarium, and the relation of the plates of the neck segment to the cephalic capsule and the gnathochilarium on the one hand, and to the body on the other.

The gnathochilarium has been variously regarded as representing the first maxillae, the second maxillae, and both pairs of maxillae combined. Silvestri (1903) contends that the gnathochilarium is the united first maxillae. According to Robinson (1907), however, there are present in the embryo of *Archispirostreptus* separate rudiments of first and second maxillae, but the first disappear, and the second alone unite to form the gnathochilarium. In a more recent study on *Platyrrhacus amauros*, Pflugfelder (1932) asserts that, while two pairs of maxillary appendages are present, they are both combined in the gnathochilarium. The last two writers thus agree as to the number of primary head appendages that are present, but they differ with respect to the segmental connections of these appendages. Robinson assumes that the segment of the gnathochilarium is contained in the head capsule; the neck segment, she says, is represented in the embryonic nervous system by a pair of postmaxillary ganglia. Pflugfelder, on the other hand, claims that the second maxillary components of the gnathochilarium are the appendages of the neck segment, and that the first true body segment is that bearing the first pair of legs. Silvestri also regards the neck segment as the somite of the second maxillae of other arthropods, but he believes that these appendages are absent in the Diplopoda. If the gnathochilarium belongs to the neck segment, its muscles should arise in this segment, whereas, according to the description of the head and neck muscles of Diplopoda given by Silvestri (1903), the muscles of the gnathochilarium take their origin within the head capsule, and the posterior musculature of the head arising on the back plate of the neck segment is very similar to the prothoracic head musculature of insects. There seems to be little support for Silvestri's view that the second maxillae of the diplopods are absent.

Considering the general similarity of the diplopod head to the cranial capsule of other arthropods, and the evidence of fundamental unity in structure between the several groups of progoneate myriapods, the current view (see Attems, 1926) is here accepted that the diplopod head contains both the first and the second maxillary somites, and that the legless neck segment is the first body somite, homologous with the first leg-bearing segment of the Symphyla. The legs of this segment are small and reduced by the loss of one segment in Symphyla; in Pauropoda, if present at all, they are rudimentary; in Diplopoda they are absent. The genital apertures of the diplopods, we may therefore conclude, are on segment *VII* behind the mouth, as in the pauropods and symphylids.

The genital openings in both sexes of the diplopods are more or less closely associated with the bases of the legs of the genital seg-

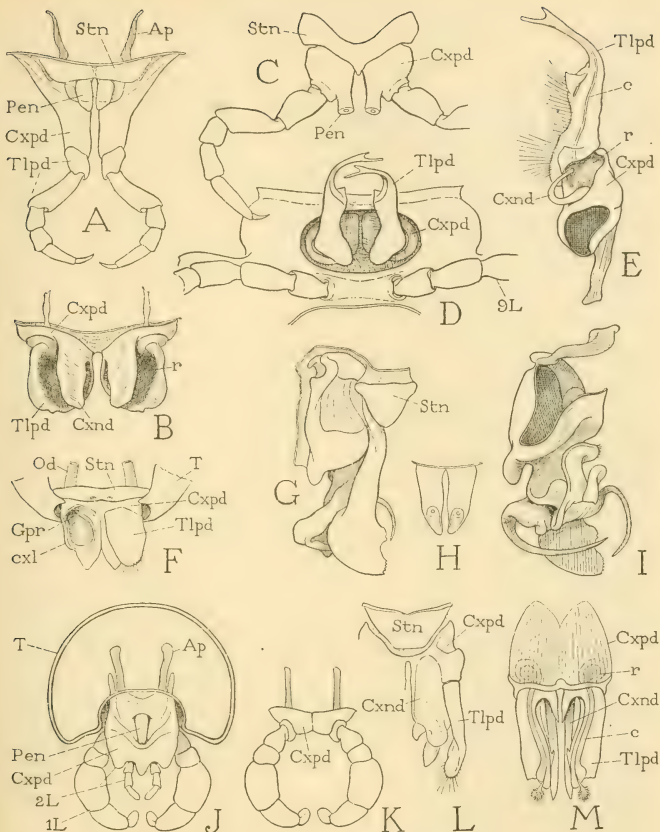


FIG. 19.—Diplopoda: external genitalia.

A, *Habrostrepsus*, male, sternum, legs, and penes of third body segment, posterior view. B, same, gonopods, anterior (under) surface. C, *Euryurus*, male, sternum, legs, and penes of third body segment, anterior view. D, same, seventh body segment, ventral view, showing position of gonopods and legs. E, same, right gonopod, anterior (upper) surface. F, *Parajulus impressus*, female, ventral part of third body segment and appendages, anterior view, telopodite of right appendage removed exposing gonopore on the coxopodite. G, *Thyropygus*, male, right gonopod, anterior (under) surface. H, same, penes, posterior surface. I, same, left gonopod, posterior (upper) surface. J, *Parajulus impressus*, male, third body segment and appendages of second segment, posterior view. K, same, appendages of second body segment, posterior surface. L, same, sternum and first gonopod of seventh body segment, anterior surface. M, same, second gonopods, posterior surface.

Ap, apodeme; c, sperm canal of gonopod; cxl, coxal lobe; Cxnd, coxal endite; Cxpd, coxopodite; Gpr, gonopore; 1L, first leg (on second body segment); 2L, second leg (on third body segment); 9L, ninth leg (second leg of seventh body segment); Od, oviduct; Pen, penis; r, sperm receptacle of gonopod; Stn, sternum; T, tergum; Tlpd, telopodite.

ment (fig. 19 C, F). The male ducts usually discharge separately on a pair of, small penes having the form of papillae or lobes arising either directly from the coxae of the second legs (*C, Pen*), or mesally behind the coxal bases (*A*), but in some forms the ducts open together on a median penis arising between or behind the legs (*J, Pen*). The legs of the genital segment in most cases have the typical leg form (*A, C*), but they may be reduced in size and otherwise modified, or united at their bases (*J, Cxpd*). In certain species the first legs also are modified in a manner suggestive that they take some part in copulation (*J, 1L, K*).

The female genital ducts open either on the coxae of the legs of the genital segment, or on the sternal surface behind the leg bases. Usually the legs of the genital segment are not modified in the female, but there are exceptions, as shown in *Parajulus impressus* (fig. 19 F), in which the telopodites of the genital appendages are reduced to small lobes (*Tlpd*) and the oviducts open into large cavities on extensions of the united coxopodites (*Cxpd*). In forms in which the ducts open behind the legs, the apertures are usually contained in a complicated integumental structure (see Brölemann and Lichtenstein, 1919, and Seifert, 1932).

Intromission is accomplished in the ordinary diplopods (Proterandria) by the modified legs (gonopods) of the seventh body segment of the male, which transfer the sperm from the penes or penis of the third segment into the genital apertures of the female. In two of the diplopod groups, however, the relatively generalized Pselaphognatha and the Opisthandria, according to the classification of Attems (1926), none of the appendages is modified for the purpose of intromission, though in members of the first group the coxae of the eighth legs have external pouches, which Attems suggests may have some reproductive function. In the Opisthandria one or two pairs of legs at the posterior end of the body in the male are specially modified to serve as copulatory organs. With these legs the male is said to grasp the genital coxae of the female, while he inserts the spermatozoa into the female gonopores with his mandibles (Attems, 1926).

The gonopods of the seventh body segment of proterandrious male Diplopoda are analogous in their function to the gonopods of malacostracan Crustacea and the pedipalps of male spiders; in their structure even they are not dissimilar from these organs. The pair of appendages converted into gonopods is usually the first pair of legs of the seventh segment; the second legs of this segment are generally of usual form, but they may be absent, or modified also to form a second pair of gonopods. A typical diplopod gonopod (fig. 19 E)



consists of two segments, a basal coxopodite (*Cxpd*), and a distal telopodite (*Tlpd*). The essential feature of the organ is a *sperm receptacle* (*r*), which is an invagination cavity on the morphologically anterior surface of the coxopodite, and a *sperm canal* (*c*), which is usually a closed groove that traverses the telopodite from the sperm receptacle to the apex of the appendage. The coxopodite is generally provided with a movable endite lobe (*Cxnd*) of various shapes, which projects over the sperm receptacle, and when slender may be partly inserted into the proximal opening of the sperm canal. The bases of the appendages are often sunken into a deep cavity on the ventral surface of the body segment (*D*). The gonopods are subject to endless modifications in form, and their structural diversity in different genera and species furnishes valuable characters in diplopod taxonomy.

An example of gonopods having a highly diversified and complex structure is shown in the genus *Thyropygus* (fig. 19 G, I). A very much simplified structure, on the other hand, is found in *Habrostrepus* (*B*), in which the telopodite (*Tlpd*) of each gonopod has the form of a short broad lobe with a wide, basinlike sperm cavity (*r*) on its ventral anterior surface, which is partly covered by a flat endite lobe (*Cxl*) of the coxa. In some forms, as in *Parajulus* (*L*, *M*), both pairs of legs of the seventh body segment are transformed into gonopods, the second of which in this case contain the sperm receptacles (*M*, *r*) and canals (*c*). More extensive and detailed descriptions of the diplopod gonopods will be found in works by Vosges (1878), Verhoeff (1903), Silvestri (1916), Attems (1894, 1926), and Siefert (1932); the last writer gives also an account of the manner of copulation and insemination in *Polydesmus edentulus*.

#### IX. CHILOPODA (MYRIAPODA OPISTHOgoneata)

The Chilopoda have a single median genital aperture, which in each sex is always behind the sternum of the last somite, that is, between the penultimate body segment and the anus-bearing end segment, or telson. The number of segments anterior to the genital segment, however, is so variable in the chilopods as a whole that no fixed numerical designation can be given to the genital segment itself. In the anamorphic forms (*Lithobius*, *Scutigera*), in which the adult segmentation does not vary, there are 19 definitive body segments, including the telson. Counting four postoral somites in the head, the genital segment in this group, therefore, is somite XXII. Among the Epimorpha, in which the definitive segmentation is in most forms complete at hatching, the number of segments is highly variable in the Geophilomorpha, even in the same species, and may be very large,



while in Scolopendromorpha there are either 26 or 28 body segments, but the number is constant for each species.

The gonads of the Chilopoda lie above the alimentary canal, as in Crustacea and Hexapoda, whereas in the progoneate myriapods they lie below the alimentary canal. The testes in Epimorpha consist of from 1 to 12 pairs of short spindle-shaped tubes each united at each end by a slender ductule with a common median gonoduct. Among the Anamorpha, *Lithobius* has a single median tubular testis, but *Scutigera* has two slender testicular tubes. The ovaries are in all forms united in a single median tubular gonad, in the walls of which the germ cells are arranged in a longitudinal band or a pair of lateral bands. The median gonoduct of each sex is apparently a ductus conjunctus; posteriorly it divides into two arms that embrace the rectum and unite again below it in a short exit or genital chamber, into which open one or two pairs of accessory glands, and in the female a pair of seminal receptacles. The left branch of the gonoduct in the Epimorpha becomes reduced or rudimentary, and only the right branch serves as the functional exit tube.

The external genital region of the chilopod body consists of two small legless segments intercalated between the last leg-bearing segment and the terminal anus-bearing telson. These segments, which in the Epimorpha are differentiated during embryonic development as two very small somites (fig. 20 A), are termed by Heymons (1901) the *pregenital segment* (*1gSeg*) and the *genital segment* (*2gSeg*). The two segments may bear each a pair of small or rudimentary appendages, which are the *first* and the *second gonopods* (*1Gp*, *2Gp*). The definitive genital opening is formed behind the sternum of the genital segment; the gonopore is usually concealed in a genital chamber, but in the male it is on a small protractile penis. In the Anamorpha, which add segments during postembryonic development from a generative zone before the telson, the genital segments are the last to be formed. The definitive segmentation of the chilopod body, therefore, depends on the number of somites generated before the establishment of the genital segments, after which there is no further somite propagation. The variable number of pregenital segments generated in the Chilopoda from a postgenital zone of growth, as already noted, must lead to the conclusion that the two segments in the definitive genital region are not homologous somites in all cases, notwithstanding their similarity of structure. However, the structure of these two segments is probably only that which any segments might take on if arrested in their growth at an early stage of development.

The most generalized condition of the genital region in the adult chilopod is found in the Geophilomorpha, in which both genital sterna

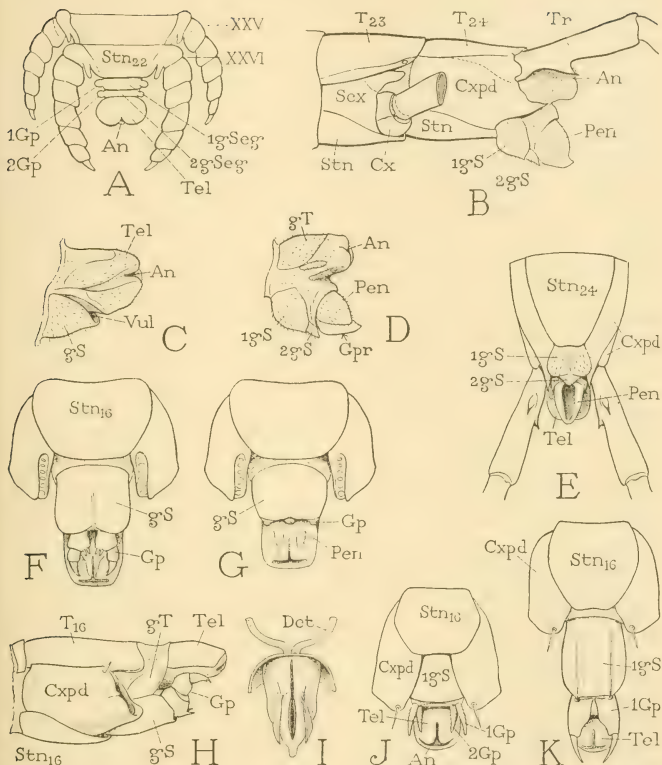


FIG. 20.—Chilopoda: external genitalia.

A, *Scolopendra*, posterior end of body of embryo, showing two small segments in genital region between last leg-bearing segment and telson (from Heymons, 1901). B, *Scolopocryptops*, male, terminal part of body with penis protracted. C, same, female, genital and anal segments. D, same, male, genital and anal segments, lateral view. E, same, male, posterior end of body, ventral view. F, *Lithobius*, female, posterior end of body, ventral view. G, same, corresponding segments of male. H, same, female, lateral view of posterior body segments. I, same, male, ventral view of penis and ducts. J, *Scutigera forceps*, male, posterior end of body, ventral view. K, same, corresponding segments of female, ventral view.

An, anus; Cr, coxa; Cxpd, coxopodite; Dct, genital duct; Gp, gonopod; 1Gp, 2Gp, first and second gonopods; gS, genital sternum; 1gS, 2gS, first and second genital sterna; 1gSeg, first genital, or pregenital, segment; 2gSeg, second genital, or genital, segment; gT, genital tergum; Pen, penis; Scx, subcoxa; Stn, sternum; T, tergum; Tel, telson; Tr, trochanter.

are distinct, though only the second bears a pair of small, sometimes two-segmented gonopods, and the terga of the two segments are united in a single dorsal plate. In other forms the second sternum is either much reduced or obliterated, but the gonopods of the first segment or of both segments may be present. Both genital sterna appear to be retained in the male of *Scolopocryptops* (fig. 20 B, D, E), though the second (*2gS*) is very small and is absent in the female (C). A single tergal plate covers the back of the genital region of the male (D, *gT*). Neither pair of gonopods is represented, but a large median penis (B, D, E, *Pen*) is protractile from a bursa genitalis (genital chamber) invaginated above the genital sterna. In *Lithobius* there is a single large genital sternum in each sex, which presumably is that of the first genital, or pregenital, segment (F, G, *gS*). A pair of well-developed, three-segmented gonopods is present in the female of the species figured (F, H, *Gp*), but in the male (G) the appendages are rudimentary. The penis is a small conical organ opening ventrally by a median slit (I), and is ordinarily almost entirely concealed in the bursa genitalis (G). The male of *Scutigera forceps* (J) has two pairs of styluslike gonopods, the first borne by the pregenital sternum (*1gS*), the second by a small membranous fold possibly representing the venter of the second genital segment. In the female (K) only the anterior gonopods are present, but these appendages have the form of long two-segmented claspers borne by the large pregenital sternum (*1gS*). Copulation in the chilopods has not been observed, but the males of some species are known to produce spermatophores, and spermatozoa are found in the seminal receptacles of the female.

The chilopods resemble the hexapods in the possession of a median penis and in the modification of the appendages in the genital region to form accessory reproductive organs. The fact, however, that quite different somites may be involved in the development of the genital complex eliminates the question of homology between the parts, and the superficial likeness in the external genitalia of the Chilopoda and Hexapoda is thus no evidence of close relationship between these two groups.

## X. HEXAPODA

The fundamental feature in the structural organization of the Hexapoda that distinguishes the six-legged arthropods from members of all other arthropod groups is the concentration of the locomotor mechanism in the three body segments immediately following the fourth postoral somite. The Hexapoda, therefore, include the Protura and Collembola as well as the ordinary insects. The number of seg-

ments behind the locomotor region, or thorax, is inconsequential, as is also the matter of whether the abdominal segmentation is completed before or after hatching.

The hexapods are always opisthogoneate in that the genital ducts extend posteriorly from the gonads and open near the end of the body, but there is considerable variation in the number of somites that precede the genital somite. In the Collembola the genital opening in each sex is at the posterior end of the fifth abdominal segment, which is segment *XII* from the mouth, and there is only one postgenital segment. The genital openings in Protura are likewise at the end of the penultimate segment, but this segment is somite *XVIII* (eleventh abdominal segment). In insects other than Collembola and Protura the primitive paired gonopores were probably in the female on somite *XIV* (seventh abdominal segment), and in the male on somite *XVII* (tenth abdominal). With most of the insects, however, the definitive genital outlet is the aperture of a secondary median duct, and is subject to migration in the female from the seventh abdominal segment to the eighth, ninth, or tenth, but in the male appears to be always between the ninth and tenth segments.

Considering the fact that somite formation is teloblastic in the arthropods, and that the generative zone lies just before the end-segment, or telson, it is evidently impossible that the genital segment can be the same somite in Collembola, Protura, and the other insects. With the establishment of the genital ducts in Collembola and Protura, somite formation has ceased, but the genital segment in the former is the fifth abdominal somite, and in the latter the eleventh. With the other insects, four embryonic somites may be generated in the female behind the segment of the primary genital ducts, and one in the male. The abdomen of all the hexapods except Collembola has thus become standardized with a maximum segmentation of eleven somites between the thorax and the telson; but the telson, except in Protura, is suppressed in the adult and the eleventh somite forms the usual proctiger, though it too is often reduced or united with the tenth. The reason for regarding the twelfth abdominal segment of the Hexapoda as the telson is that, when present in the embryo, it never has any of the appurtenances of a somite, such as appendages or nerve ganglia.

The lateral gonoducts of the male have separate openings to the exterior among the Hexapoda in Protura, Ephemeroptera, some Dermaptera, and perhaps secondarily in certain Diptera; but in general the lateral ducts discharge into a median ductus communis. Embryological evidence (see Heymons, 1895, 1897; Wheeler, 1893) gives reason for believing that the primary genital ducts of male

insects opened originally on segment *XVII*, which is the tenth abdominal segment (fig. 21 A, *Vd*), and that very probably the gonopores were located on the bases of the segmental appendages, as is the case in many other arthropods. The usual common exit duct, ductus ejaculatorius (B, *Dej*), is formed ontogenetically as a median invagination at the posterior margin of the venter of the ninth abdominal segment. Anatomically the point of origin of the ejaculatory duct

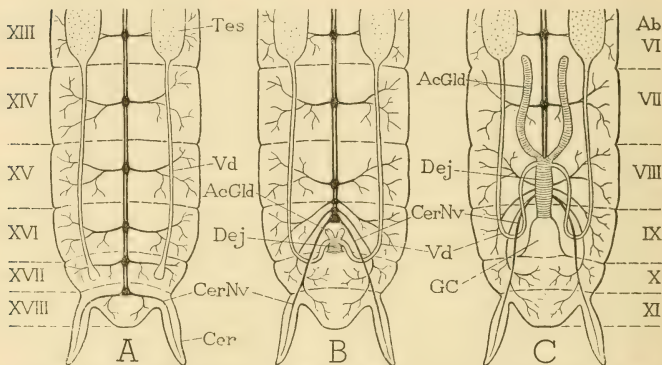


FIG. 21.—Diagrams showing the relation of the male genital ducts in Orthoptera to the nerves of the tenth and eleventh abdominal segments.

A, primitive stage: vasa deferentia (*Vd*) opening separately on tenth abdominal segment (postoral somite *XVII*) between the lateral nerves of tenth and eleventh segments. B, later stage: vasa deferentia opening medially into an ejaculatory duct (*Dej*) invaginated at posterior end of ninth abdominal segment; last three ganglia of nerve cord moved forward, drawing the cercal nerves (*CerNv*) over the genital ducts. C, definitive stage: the last four ganglia united in eighth abdominal segment; genital exit system extended forward by growth of ejaculatory duct and addition of genital chamber (*GC*), the vasa deferentia looped beneath the cercal nerves.

*Ab*, abdominal segments; *AcGld*, accessory genital gland; *Cer*, cercus; *CerNv*, cercal nerve; *Dej*, ductus ejaculatorius; *GC*, genital chamber; *Tes*, testis; *Vd*, vas deferens; *VI-XI* (on right), abdominal segments; *XIII-XVIII* (on left), postoral somites.

appears thus to be intersegmental between the ninth and tenth abdominal segments, but some incomplected observations made by the writer on the innervation of the genital organs in Orthoptera seem to indicate that the ductus ejaculatorius derives its innervation from nerve trunks that pertain to the tenth segment. It is possible, therefore, that the median genital duct of the male morphologically belongs to the tenth abdominal somite. Perhaps the median duct was primarily the outlet of the accessory genital glands (B, *AcGld*), but, whatever its



original nature may have been, since the vasa deferentia come to open into its anterior end at the bases of the glandular diverticula, the median duct of the male becomes the exit both for the secretion of the accessory glands and for the spermatozoa. The mouth of the common duct is the median gonopore of the male. The gonopore may be exposed on a small phallic papilla arising from the ventral membrane between the ninth and tenth abdominal segments, but generally this membrane is invaginated to form the male bursa genitales, or genital chamber (C, GC), and the gonopore is then carried out upon a tubular evagination of the anterior wall of the chamber, which forms the usual phallic organ.

A study of the anatomical relations between the vasa deferentia and the posterior segmental nerve trunks of the abdomen in Orthoptera shows that the male genital ducts must originally have crossed over the lateral nerves of the tenth abdominal segment and attached to the ectoderm behind these nerves (fig. 21 A, *Vd*). The subsequent union of the vasa deferentia with the median ductus ejaculatorius (B), however, necessitated a median and forward migration of the posterior ends of the lateral ducts. The correlated forward retraction of the posterior part of the ventral nerve cord then drew the large nerves of the cerci (*CerNv*), given off from the terminal ganglion, over the incurved ends of the vasa deferentia (*Vd*). Hence, in the definitive condition (C), the vasa deferentia are always looped beneath the cercal nerves, but lie dorsal to the other lateral nerve trunks of the abdomen. This condition could follow only from one in which the primitive genital ducts turned downward to the body wall between the nerve trunks of the tenth and eleventh abdominal segments (A). Likewise, in female Orthoptera, the relation of the lateral oviducts to the nerve trunks shows that the primitive lateral ducts must have opened somewhere between the nerves of the seventh and eighth abdominal segments. Incidentally, the nerve-duct relation in the male demonstrates also that the cerci are appendages of the eleventh abdominal segment.

The paired penes of the Hexapoda are best shown as simple independent structures in some of the Ephemeroptera (fig. 25 C, *Pen*). They are supported on basal arms or a basal plate (C, F, *x*), which possibly may represent the sternum of the tenth abdominal segment. Since there are no true appendages on the tenth segment, there is no evidence as to what relation the penes may have had to the limb bases, but, judging from other arthropods, there is no reason to suppose that the primitive penes of the hexapods were structures other than papillae of the coxopodites containing the outlets of the genital ducts.



Among the mayflies as well as in the Protura and Dermaptera the penes show a tendency to combine into a single organ (penis conjunctus) as they do also in some Crustacea and Diplopoda.

The usual median intromittent organ, or phallus, of adult insects is evidently a *penis communis*, since neither in its structure nor its ontogeny is there any evidence that the organ has been produced by the union of a pair of rudiments containing the outlets or ends of the lateral genital ducts. It is formed as a tubular outgrowth of the body wall around the mouth of the ejaculatory duct, or by the union of phallic lobes that enclose the gonopore. The theory suggested by Crampton (1920), and formerly accepted by the writer (1931, p. 91), that the phallus has been evolved in part or entirely from mesal lobes of the appendages of the ninth abdominal segment, appears to be quite without anatomical or ontogenetic foundation. The genital appendages are variously and often highly developed, but they take no part in the formation of the phallus.

The phallic organ of insects is subject to endless variations in form, and it is not to be supposed that the numerous accessory structures encountered, or even the more general modifications are necessarily homologous developments in different groups of insects, for it must unquestionably be true that, with apparently unlimited variation, similar forms have been many times produced quite independently. Furthermore, as will later be shown, it is very probable that the median penis itself has been evolved in different ways in several insect groups. The musculature of the phallus, even among closely related insects, is so highly variable and so evidently adaptive in its nature, that it cannot be used for determining anatomical relationships or homologies in the phallic structures.

The intimate association of the phallus with the ninth abdominal segment has involved this segment so closely in the genital function that usually it is the segment of the genital region most affected by structural modifications adaptive to the mechanism of copulation and intromission. The ninth segment, in fact, may be designated *the genital segment* of male insects. The neighboring segments, however, are often variously modified also as parts of the genital complex, and in the higher Diptera all the segments beyond the fifth form a distinct genital section of the abdomen. A point that should be emphasized in the study of the male genitalia of insects, particularly in Orthoptera, is the fact that the structure of the phallic organ and of the genital segment is not necessarily, in its principal aspect, an adaptation to the functions of copulation and intromission, but may be very largely concerned with the formation of spermatophores and the transference of the latter to the female.

The male bursa genitalis, or genital chamber, which usually contains the phallic organ or organs, projects into the ninth abdominal segment (fig. 22 A, *GC*) since it is an invagination of the integument behind the ninth sternum, though its dorsal wall presumably belongs to the venter of the tenth segment. Appendages of the ninth segment (gonopods) may be entirely absent; in Orthoptera and some related insects they are small styluslike structures resembling the abdominal styli of Thysanura, though unlike the latter they are not provided

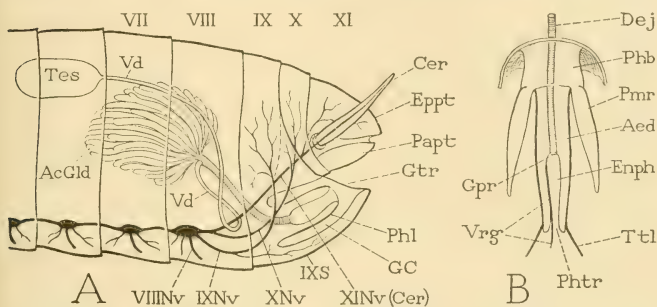


FIG. 22.—Diagrams of the position and structure of the external and internal genitalia of male insects.

A, general position and relation of the male reproductive organs of orthopteroid type. B, diagram of the median penis, or phallus, showing parts that commonly recur, but which are not necessarily or usually present in the same species.

*AcGld*, accessory genital gland; *Aed*, aedeagus; *Cer*, cercus; *Dej*, ductus ejaculatorius; *Enph*, endophallus; *Eppt*, epiproct; *GC*, genital chamber, or bursa genitalis; *Gpr*, gonopore (aperture of ejaculatory duct); *Gtr*, gonotreme (opening of genital chamber); *IXS*, sternum of ninth abdominal segment (male subgenital plate, hypandrium); *Papt*, paraproct; *Phb*, phallobase; *Phl*, phallus (median penis); *Phtr*, phallotreme (distal opening of endophallus); *Pmr*, paramere; *Tes*, testis; *Ttl*, titillator, *Vd*, vas deferens; *Vrg*, virga; *VII-XI*, seventh to eleventh abdominal segments; *VIII<sub>Nv</sub>*, *IX<sub>Nv</sub>*, *X<sub>Nv</sub>*, *XI<sub>Nv</sub>*, principal lateral nerves of eighth, ninth, tenth, and eleventh abdominal segments issuing from composite last ganglion of ventral nerve cord.

with muscles. In many of the higher insects, however, the appendages of the male genital segment take the form of large movable organs of various shapes usually adapted to grasping or holding the female. These genital claspers (valvae, harpes, harpagones) are always distinguishable from other similar but immovable or merely flexible lobes or processes borne on the ninth or other segments of the genital complex by the fact that they are independently movable by muscles inserted on or in their bases. Such appendages are most probably homologues of the thysanuran abdominal styli. In some cases the movable claspers are supported on distinct basal plates, but more commonly

the basal segments (coxopodites) of the gonopods of pterygote insects are incorporated in the wall of the segmental annulus. The movable claspers, together with the other genital processes that arise peripherally from the segments of the genital region, may be designated collectively the *periphallic organs*.

#### DEFINITIONS OF EXTERNAL GENITAL STRUCTURES OF THE MALE

The principal parts of the external genitalia and their commonly developed accessories in male insects and other arthropods may be named and defined as given in the following list of terms, but no general nomenclature can be devised to include names for all the minor modifications and special developments found in the various orders of insects.

*Aedeagus* (*Aed*).—The distal part of the phallus when the latter has a differentiated basal part; usually the principal part of the phallus, or the entire organ if the phallobase is suppressed; typically a sclerotic tube with the phallotreme at its extremity.

*Bursa genitalis* (*GC*).—The genital chamber of either the male or the female; in male insects a ventral invagination of the membranous integument behind the ninth abdominal sternum containing the phallus or phallic organs.

*Copulatory organs*.—Any structures used by either sex for grasping or holding the partner during mating, or particularly paired organs, usually segmental appendages, specially adapted or modified for copulatory purposes.

*Ductus ejaculatorius* (*Dej*).—The median exit duct of the male genital system; if formed by the union of a pair of primary ductus ejaculatorii it is a *ductus conjunctus*, if developed as a single median invagination of the integument serving as an outlet for both vasa deferentia it is a *ductus communis*.

*Ectophallus*.—The outer wall or exposed part of the phallus in distinction to the endophallus.

*Endophallus* (*Enph*).—An inner phallic chamber invaginated at the end of the ectophallus, and containing the true gonopore, or opening of the ejaculatory duct; typically an eversible sac or tube, often mistaken for the end of the ejaculatory duct, but sometimes a permanently internal phallic structure that may attain a complex development. (*Preputial sac*.)

*Endotheca* (*Enth*).—The inner wall of the phallotheca.

*Epimere*.—A dorsal process of the phallobase.

*Epiphallus* (*Epph*).—A large, transverse sclerite developed in the dorsal wall of the base of the phallus, characteristic of Acrididae. (*Pseudosternite* of Walker.)

*Genital chamber* (*GC*).—See *bursa genitalis*.

*Genital segment*, or *gonosomite*.—Specifically the body segment bearing the openings of the primary genital ducts, or the segment with which the median gonopore is most closely associated, but also in a wider sense any one of the segments in a specially differentiated genital region of the body. In insects the genital segment is primarily the seventh abdominal somite in the female and the tenth in the male, but secondarily the female genital segment is usually the eighth or the ninth abdominal somite, and that of the male the ninth.

*Gonapophysis* (*Gon.*).—Any part of a segmental appendage closely associated with the genital segment and having some function intimately related to intromission of the sperm by the male or the deposition of eggs by the female. In male Malacostraca the gonapophyses are the endopodites of the first and second abdominal appendages and serve as intromittent organs; in insects the gonapophyses are apparently endites of the appendages of the eighth and ninth abdominal segments, present in both sexes of some Thysanura, forming the usual ovipositor of female insects.

*Gonopod* (*Gp*).—An appendage of the genital segment or of an associated segment modified for some purpose in connection with copulation, intromission, or oviposition.

*Gonopore* (*Gpr*).—The external opening of a genital duct, whether exposed, or concealed in a secondary invagination of the integument, such as the genital chamber or an endophallic cavity.

*Gonostyli*.—The styli of the ninth abdominal segment of some male insects, presumably appendicular parts of the coxopodites of the gonopods, probably homologous with the movable claspers (*harpagones*) of many insects.

*Gonotreme* (*Gtr*).—The external opening of the bursa genitalis, or genital chamber, in either sex; the *vulva* of the female.

*Harpagones* (*Hrp.*).—Movable periphalllic appendicular organs of the ninth abdominal segment of the male, individually provided with muscles, probably derivatives of the gonostyli, sometimes supported on distinct coxopodite plates. (*Valvae*, *harpes*.)

*Hypandrium* (*IXS*).—The subgenital plate of the male, usually the sternum of the ninth abdominal segment.

*Hypomere*.—A ventral process of the phallobase.

*Intromittent organs*.—Any structure of the male serving for the introduction of the sperm or spermatophores into the female, in some

cases the paired penes, in insects usually the median penis, or phallus, but in many other arthropods modified appendages that assume the intromittent function, as in Araneida, Malacostraca, and Diplopoda.

*Parameres* (*Pmr*).—Lateral processes or lobes of the phallobase, probably secondary outgrowths having no relation to the gonopods.

*Penis* (*Pen*).—A general term applied to any integumental outgrowth containing the orifice of a male genital duct, whether intromittent in function or not, including the paired penes of many arthropods, or a median penis (phallus); but the term is often used also in a restricted functional sense for the part of the phallus or any other intromittent organ inserted into the female genital receptacle during mating. The primitive paired penes of most arthropods are on the bases of a particular pair of segmental appendages, or on the sternum mesad of the appendages. A median penis may be either a *penis conjunctus* or a *penis communis* according as it is formed by the union of a pair of penes, or by a secondary median outgrowth of the integument.

*Periphallic organs*.—Peripheral genital processes of the ninth segment or of other segments in the male genital complex of insects, including the movable claspers, or harpagones.

*Phallic organs*.—The median genital structures of male insects immediately concerned with the function of coition, or the introduction of the spermatozoa or spermatophores into the receptacular organ of the female; the phallic organs are highly variable, and are formed ontogenetically in various ways, but always independently of the periphallic organs.

*Phallobase* (*Phb*).—A differentiated basal part of the phallus, variable and often not distinct from the aedeagus. (*Tegmen* in Coleoptera.)

*Phallocrypt* (*Crpt*).—A pocket of the phallobase or of the genital chamber wall containing the base of the aedeagus or of the ectophallus.

*Phallomeres* (*Phm*).—Phallic organs having the form of lobes produced from the genital chamber wall in the neighborhood of the gonopore; particularly developed in Blattidae and Mantidae, probably united in the median phallic organ of other Orthoptera, and perhaps represented by lobes that form the phallus in the ontogeny of some higher insects.

*Phallotheca* (*Thc*).—A fold sometimes extended from the phallobase around the base of the aedeagus, or produced as a tubular sheath enclosing the latter, in exceptional cases replacing the aedeagus.

*Phallotreme* (*Phtr*).—The distal opening of the endophallus at the extremity of the ectophallus, the functional exit aperture of the genital tract when the true gonopore is contained in an endophallic chamber.



*Phallus* (*Phl*).—The usual median penis or single intromittent organ of male insects, variously formed and probably developed independently in several insect groups.

*Preputial sac*.—See *endophallus*.

*Subgenital plate* (*IXS*).—See *hypandrium*.

*Titillators* (*Ttl*).—Distal external processes of the aedeagus.

*Virga* (*Vir*).—A terminal phallic spine or slender rod usually arising from the wall of the endophallus and therefore protractile with the eversion of the latter.

#### COLLEMBOLA

The Collembola are hexapods with a differentiated thorax and abdomen, but having at most only six abdominal segments. Their embryology gives no evidence of a greater number of somites ever having been present, which fact is surprising considering that the immediate ancestors of all the other hexapods undoubtedly had a standardized abdomen of 12 segments. The single genital opening in each sex of the Collembola is on the extreme posterior part of the venter of the fifth abdominal segment; the gonopore thus has the same position relative to the terminal segment as has the genital opening in Chilopoda and Protura, but the disparity in the number of somites preceding the genital segment shows that the subterminal position of the gonopore in these three arthropod groups is not a matter of anatomical homology. The genital aperture of the Collembola is situated sometimes on a slight elevation of the integument, but there is no development of the external genital region sufficient to constitute an intromittent organ or an ovipositor.

The internal reproductive organs of Collembola have been studied by Sommer (1885), Fernald (1890), Willem (1900), Lécaillon (1901, 1902, 1902*a*, 1902*b*), Imms (1906), and De Winter (1913). The gonads lie ventro-laterally in the abdomen and the posterior part of the thorax (fig. 23 A), and in the mature condition they approximate each other *beneath* the alimentary canal (C, G). The testes are continuous posteriorly with short lateral ducts that join a common exit duct (A, B, *Dej*), the anterior end of which may be enlarged as a seminal vesicle (B, *Vsm*).

In the younger stages of all Collembola, according to Willem (1900), the gonads are simple fusiform sacs, each tapering anteriorly to a suspensory ligament; as development progresses, however, the organs in most cases lose their primitive form, become greatly enlarged, and variously modified in shape (fig. 23 F, G). The germinal area of each organ in some forms is situated in the dorsal or



lateral wall of the gonadial sac (B, D, G, *Grm*), and in this feature the gonads of certain Collembola preserve the generalized structure of the reproductive organs found in Onychophora, and in arthropods

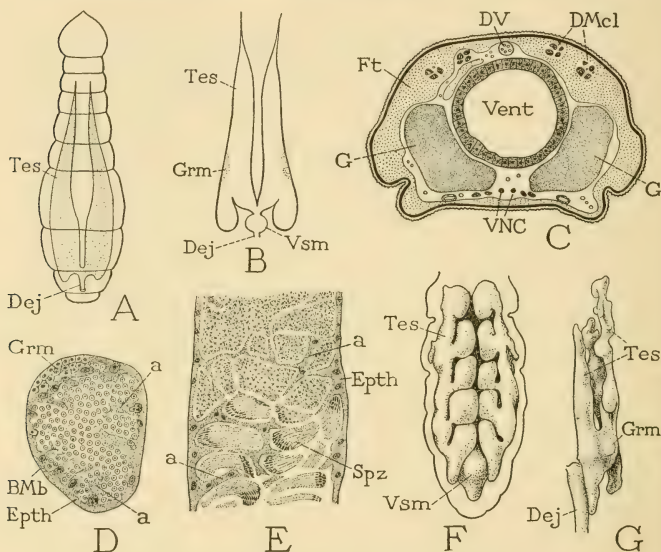


FIG. 23.—Hexapoda-Collembola: internal genitalia.

A, *Anurida maritima*, diagram of position of male gonads (from Imms, 1906). B, *Anurophorus laricis*, outline of testes showing position of germaria (from Lécaillon, 1902a). C, *Anurida maritima*, transverse section through fourth abdominal segment (from Imms, 1906). D, *Anurophorus laricis*, transverse section of testis, showing germarium in dorsal wall (from Lécaillon, 1902a). E, *Anurida maritima*, longitudinal section of posterior part of testis, showing bundles of spermatozoa separated by ingrowths of epithelial wall (from Imms, 1906). F, *Podura aquatica*, mature testis, dorsal view (from Willem, 1900). G, *Tomocerus vulgaris*, mature testis of right side, dorsal view (from Willem, 1900).

a, intratesticular ingrowths of testicular epithelium; BMB, basement membrane; Dej, ductus ejaculatorius; DMcl, dorsal longitudinal muscles; DV, dorsal blood vessel; Epth, testicular epithelium; Ft, fat tissue; G, gonad; Grm, germarium; Spz, spermatozoa; Tes, testis; Vent, ventriculus; VNC, ventral nerve cord; Vsm, vesicula seminalis.

other than insects in which the germinal cells have not become localized in the apex of the gonads or in the apices of lateral diverticula. Within the lumen of the testis the bundles of developing spermatozoa (E, *Spz*) are enclosed in compartments formed of intratesticular

prolongations (*a*) from the epithelial walls (*Epth*) of the gonad. The testicular cysts of other insects are said to be formed of cells descended from the spermatogonia.

The simple shape of the gonads is most fully carried over into the adult stage in *Anurida*, in which the ovaries and testes, though they may increase greatly in size from the immature stages, retain for the most part an undivided saclike form (fig. 23 A, B). The germinal area of *Anurida*, as described by Lécaillon (1902) and by Imms (1906), lies in the dorsal wall of the gonad (D, *Grm*). In the male, Imms says, "the germinal tissue is in the form of a mass or ridge, situated at about the middle of the length of the testis", in the female it forms in each ovary "a protruding ridge lying in the region of the third and fourth abdominal segments." In *Podura*, according to Willem (1900), the adult gonads are voluminous organs occupying the abdomen and the last two segments of the thorax. Each gonad is an irregular sac (F) with its mesal wall produced into five large pouches separated by deep incisions, but the germarial zone of the testis extends through the entire length of the dorsal wall of the organ, both on the undivided lateral part and on the mesal pouches.

In the Entomobryidae, as shown by Willem (1900), the immature gonads are simple fusiform sacs as in the young of Poduridae, but in each sex the germarium is localized in the apex of the organ, evidently a secondary condition, Willem contends. As development proceeds, however, each gonad grows anteriorly and posteriorly beyond the germinal zone in each direction, with the result that in the definitive organ, the germarium is a restricted area of the lateral wall of the gonad near the posterior end of the latter (fig. 23 G, *Grm*). In this family the gonad becomes two-branched by the development of a long mesal lobe opposite the germarium. The gonads of Neelidae and Sminthuridae are undivided tubes, but each tube is bent upon itself because of the limited space in the globular abdomen. According to Lécaillon (1902) the germinal zone in the male of these families is restricted to the apex of the testis; in the female of *Sminthurus*, Willem says, the germinal region of the ovary lies ventrally in the outer wall of the middle part of the tube, but much nearer the anterior end of the latter than in Poduridae and Entomobryidae.

From the above review of the structure and development of the collembolan gonads it is evident that the organs, beginning with a generalized condition, have followed a line of specialization confined to the Collembola. The primitive gonadial sac, as represented by the testis of Poduridae, probably had a germarial band in its dorsal wall. The localization of the germarium in the apex of the gonad in other

forms is, therefore, as Willem contends, a specialized condition; it results in the formation of a gonad resembling a single testicular or ovarian tube of Thysanura and Pterygota, but which cannot be a morphological counterpart of the latter, since the tubes of a compound gonad are developed as lateral outgrowths of the primitive sac.

The development of the eggs in the ovary of *Podura* is described by De Winter (1913), who shows that the oocytes are proliferated in rows extending peripherally from the germarium, and that they become enmeshed in a reticulum of cells that grow inward from the outer epithelium of the ovary. The distal oocytes, by reason of their closer contact with the blood, are the better nourished and develop into the functional ova, while the more central cells become degenerate, and some of them in contact with the outer cells are absorbed by the latter. The general structure of the ovary of *Podura*, with the peripheral development of the ova, and the close resemblance to the ovary of *Lithobius*, De Winter contends, shows that the poduran ovary is not derived by condensation or reduction from the compound type of insect gonad, but is a gonad of generalized structure, and represents the most primitive type of ovary found among the insects.

No verified observations have yet been made on the exact manner of insemination of the female by the male in Collembola. The curious mating habits of the Sminthuridae, however, have long been known and have recently been described in detail by Falkenhan (1932) and by Strebel (1932). The male approaches a female and with his antennae grasps the antennae of the female, the male antennae being specially adapted for clasping by a modification of the second and third segments. The male is then lifted by the female, who carries him around suspended before or above her body while she goes about the affairs of her ordinary life. The male remains inactive with his legs folded against the body, and is thus transported by the female for a time varying from a few hours to as long as a day and a half, but with intermissions the carrying of the male may be continued for four or five days. Only one writer, Lie-Pettersen (1899), claims to have observed the act of insemination; according to his account a male while suspended by the female was seen to emit a drop of spermatid fluid, which fell on the wall of the glass tube containing the insects, whereupon the male released himself, with his fore legs smeared the drop on his mouth parts, and then inserted the latter into the genital opening of the female. Neither Falkenhan nor Strebel, after prolonged observation, saw any act on the part of the mated sminthurids such as that described by Lie-Pettersen. Falkenhan postulates, however, that insemi-

nation may take place by the emission of a drop of spermatic fluid from the male, which, falling to the ground, is taken up directly by the female into her genital orifice. There seems to be little doubt that the mating performance of the Smynthuridae is accessory to insemination, since Falkenhan finds that the eggs of females that have not been allowed to mate are infertile. Egg laying takes place ordinarily about 14 to 18 days after mating, though the time varies according to temperature and the age of the female.

#### PROTURA

The Protura, in the fully matured stage, have 12 abdominal segments, and this character would appear to relate them more closely to insects other than Collembola, in which the maximum segmentation of the abdomen, as shown in the embryos of some forms, consists of eleven somites and a telson. The Protura differ from other hexapods in that the last two somites before the end segment, or telson, are formed during postembryonic growth, as in anamorphic Chilopoda. Whether segmentation is completed before or after hatching, however, cannot be a matter of great importance, since it is variable among the chilopods themselves. The genital openings of the Protura are on the penultimate body segment as in Collembola and Chilopoda, but, as already pointed out, the genital segment, though subterminal in position, is numerically quite a different somite in each of these three groups.

The gonads of Protura lie ventral to the alimentary canal, as in Collembola, but in their structure they resemble a single gonadial tube of an insect ovary or testis of the usual compound type, in which each tube has a germarial zone at its apex. The proturan ovary or testis, as described by Berlese (1910), is a large tubular sac with the tapering anterior end folded ventrally and posteriorly. In the deflexed apical region are contained the oogonia or spermatogonia, and the rest of the tube is occupied by the developing oocytes or spermatocytes. The oocytes are arranged in a single series ending with a mature ovum as in an ovariole of other insects, and the successive stages of the maturing spermatozoa form zones of growth as in an ordinary sperm tube. The proturan gonad thus does not have the primitive or generalized structure of a collembolan or chilopod gonad, and its simplicity of form, therefore, would appear to be the result of elimination of tubes from a compound organ, as is probably the case also in certain Diplura in which the gonad consists likewise of a single egg tube or sperm tube. The vasa deferentia of Protura discharge individually through terminal ejaculatory ducts, but the oviducts come together in a short median outlet tube.

The external genitalia of the Protura consist of a large bifid organ in each sex eversible from behind the sternum of the eleventh abdominal segment. In the female the common oviduct opens between the bases of the arms of the genital organ; in the male the lateral gonoducts traverse the arms and open separately near their apices (see Berlese, 1910; Prell, 1913; Tuxen, 1931). Nothing is known of the development of the proturan genital organ; its structure suggests an origin from a pair of organs. Crampton (1918) says its two arms are "doubtless homologous" with the paired penes of Dermaptera; but the different segmental relations of the organs in the two cases (with the eleventh abdominal segment in Protura, and the tenth or ninth in Dermaptera) would preclude any question of actual homology. The female has no seminal receptacle, and the mating habits of the proturans have not been recorded.

#### DIPLURA AND THYSANURA

The compound structure of the gonad first appears among the Hexapoda in the Diplura (Entotrophica) and the Thysanura (Ectotrophica). In *Campodea* the ovaries and the testes consist each of a single tube, as do the testes of *Japyx*, but in other members of both orders the gonads are compound, the number of tubules varying from two to seven on each side. In some cases, as in the female of *Japyx*, the gonadial tubes are segmentally arranged on the duct, suggesting that the compound structure of the gonad originated by the outgrowth of segmental diverticula from an elongate gonadial sac, each diverticulum carrying in its apex a part of the original germarial band. The gonoducts discharge through a single median aperture, which in the female is between the eighth and ninth abdominal segments, and in the male between the ninth and tenth. The male gonopore may be on a small integumental papilla in the Diplura; the Thysanura have a short tubular penis.

It is from the Thysanura that we derive the best evidence for the generally accepted view that the definitive sternal plates of the insect abdomen are in most cases composite structures formed in each segment by a continuous sclerotization of the areas of the true sternum and the flattened limb bases. In *Machilis* the venter of each abdominal segment anterior to the genital region is occupied by a small, anterior, median, triangular sclerite (fig. 24, A, *Stn*), and two large lateral plates (*Cxpd*) projecting posteriorly as free lobes and united with each other behind the median sclerite. The median sclerite is presumably the primary sternum of the segment. The lateral plates appear to be the bases (coxopodites) of the segmental appendages;



each may bear distally a stylus (*Sty*), and in some species, mesad of the latter, an eversible vesicle (*Vs*). The coxal plates are present also on the genital segments (F, G), but the sternal plate is absent on the ninth segment of the male (G) and on both genital segments of the female. Styli are characteristically present on the coxopodites

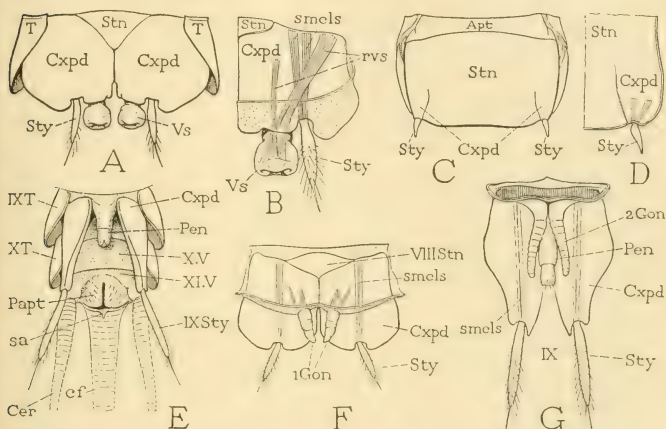


FIG. 24.—Hexapoda—Diplura and Thysanura: structure of the abdominal sterna and external genitalia.

A, *Nesomachilis maoricus*, ventral view of an abdominal segment, showing sternal surface formed of a small primary sternal plate (*Stn*) and two large coxopodite plates (*Cxpdp*) bearing appendicular organs. B, same, dorsal view of right half of sternal plates, showing muscles of vesicula and stylus. C, *Heterojapyx gallardi*, ventral view of an abdominal segment, showing coxopodites incorporated into the sternum. D, same, dorsal surface of right half of sternum, showing muscles of stylus. E, *Nesomachilis maoricus*, posterior part of male abdomen, ventral view, showing penis arising between bases of coxopodites of ninth segment. F, *Machilis variabilis*, ventral plate of eighth abdominal segment of male, with pair of small first gonapophyses (*1Gon*), dorsal view. G, same, appendages and penis of ninth segment, with second gonapophyses (*2Gon*) arising from bases of coxopodites at sides of penis.

*Apt*, sternal apotome; *Cer*, cercus; *cf*, caudal filament; *Cxpdp*, coxopodite; *1Gon*, first gonapophysis; *2Gon*, second gonapophysis; *Papt*, paraproct; *rvs*, retractor muscles of vesicula; *sa*, supra-anal lobe; *smcls*, stylus muscles; *Stn*, primary sternal plate; *Sty*, stylus; *T*, tergum; *V*, venter; *Vs*, vesicula; *VIII-XI*, abdominal segments.

of the genital segments of Thysanura, but they may be absent on the other segments; they never occur on the tenth segment, which also has no sclerotic plates in its venter (E, *XV*). The abdominal styli of Thysanura are movable by muscles arising on the coxopodite plates (B, F, G, *smcls*), but the similar processes on the thoracic coxae of *Machilis* lack muscles, as do also the abdominal styli of Orthoptera.



Rudiments of appendages have been shown by Heymons (1897) to be present on each of the first 10 segments of the abdomen in the young embryo of *Lepisma saccharina*. With the dorsal growth of the embryonic walls, however, the appendage rudiments become gradually flattened, until finally they form the lateral parts of the definitive abdominal sterna. The styli of *Lepisma*, Heymons says, are not developed until a long time after hatching, but when they do appear they arise as outgrowths from the parts of the ventral body wall derived from the embryonic appendages.

In the Diplura the styli are small if present (fig. 24 C) and are borne by the sternal plates of the segments; but the stylus-bearing areas (*Cxpd*) of each sternum may be demarked from the true sternal area (*Stn*), and upon them arise the muscles of the styli (D). From this condition it is then only another step to that in which the ventral sclerotization of a segment becomes unified in a definitive sternal plate showing no evidence of its coxosternal origin, except for the possible retention of the styli.

On the genital segments of some species of Thysanura a slender process arises at or on the inner dorsal angle of the base of each coxal plate (fig. 24 F, G, *1Gon*, *2Gon*). These four processes may be termed *gonapophyses* because those of the female, which form an ovipositor in Thysanura, are without doubt homologous with the ovipositor blades so named in other female insects. The gonapophyses of the ninth segment in male Thysanura are closely associated with the penis (G, *2Gon*) and are often termed parameres because they are supposed to correspond with accessory genital structures called parameres in other male insects (see Heymons, 1897). The term "paramere", however, has been given to many different processes of the genital complex in pterygote insects, and it is not certain that any of them is a true gonapophysis. Heymons has shown that the genital processes of *Lepisma* are formed as outgrowths from the inner margins of the coxal plates of the eighth and ninth abdominal segments. "Gonapophyses" may be defined, therefore, as mesal processes of the bases of the gonopods; they would appear to be coxal endites specially developed on the appendages of the genital segments. In the Thysanura each gonapophysis is provided with small muscles arising on the supporting coxal plate (F).

The intromittent organ of male Thysanura consists of a median tubular penis, or phallus, arising from the venter of the ninth abdominal segment between the bases of the coxal plates of this segment (fig. 24, E, G, *Pen*), where it is closely embraced by the second gonapophyses if these processes are present (G). The organ appears

to be merely a tubular evagination of the body wall with the opening of the ejaculatory duct on its extremity. It may be differentiated by a circular fold into a proximal part (phallobase) and a distal part (aedeagus).

According to Heymons (1897) the embryonic gonoducts of *Lepisma saccharina* extend first to the tenth abdominal segment in the male, and to the seventh in the female. In each case the ducts end with ampullar enlargements. With the later reduction of the tenth segment during embryonic development the ampullae of the male are transposed to the ninth segment and become attached to the ectoderm at the posterior margin of this segment. Here an ectodermal ingrowth takes place between the ampullae, in which later is formed an invagination that, uniting with the ampullae, becomes the definitive ductus ejaculatorius. It is thus evident that male Thysanura must have had primarily paired genital openings on the tenth abdominal segment, and that these primitive gonopores secondarily migrated forward and approximated each other at the posterior edge of the venter of the ninth segment. Here they acquired a common outlet by the ingrowth of a median ectodermal tube. The definitive ejaculatory duct, therefore, is a ductus communis, and not the product of a union of the ends of the primary ducts. The common genital duct of the female, Heymons says, is similarly formed by a median ectodermal invagination on the eighth abdominal segment, that is, on the first somite behind the one on which the lateral ducts primarily opened.

#### EPHEMEROPTERA

The external male genitalia of the mayflies include a pair of movable appendicular clasping organs (fig. 25 A, *Sty*) carried by the ninth abdominal segment, and a pair of small penes (*Pen*) arising behind the sternal plate of this segment. The presence of two penes in the male might be supposed to be correlated functionally with the presence of two oviducal openings in the female, but there is no evidence that coition takes place during copulation, and spermatozoa have not been found in the oviducts of the female (a spermatheca being absent). It seems very probable, therefore, that the eggs are inseminated as they issue from the oviducts, since they are carried by the female until deposited in the water. The eggs are said to be easily fertilized artificially outside the body of the female (Wiebe, 1926). The ovaries and the testes are fully developed in the last larval stage, and it is then that the sex elements are brought to maturity. Prior to mating, the eggs are massed in the greatly distended saclike calyces of the oviducts, and the spermatozoa are stored in the seminal vesicles.

The insects are thus prepared to complete the reproductive function during the brief period of imaginal life. (See Needham, Traver, and Hsu, 1935.)

The genital claspers of male Ephemeroptera are movable appendicular organs structurally comparable with the abdominal appendages of Thysanura, and the same terminology may be used in each case with the understanding that the implied homologies may still be questioned for lack of positive evidence. Each clasper of the male mayfly appears to consist of two principal parts, a distal *stylus* (fig. 25 G, *Sty*), and a proximal *coxopodite* (*Cxpd*). The stylus is movable on the coxopodite by muscles arising in the latter, and hence its identity can be determined by finding the muscles inserted on its base. The identity of the coxopodite, on the other hand, is not so easily established, since, though the stylus muscles arise in the coxopodites, the latter may become united with each other or assume various relations with the supporting sternal plate of the ninth abdominal segment.

If the genital claspers of the mayflies are homologous with the thysanuran abdominal appendages, a generalized structure of the former should be something like that shown in *Blasturus nebulosus* (fig. 25 G), in which the coxopodites are borne on the posterior margin of the ninth abdominal sternum (*IXStn*) and are partially united with each other medially (cf. fig. 24 A). The stylus muscles here arise within the coxopodites, and the coxopodites themselves are movable by muscles (*cxmcl*) arising on the sternal plate. More generally, however, the stylus muscles take their origin from a broad plate continuous across the posterior margin of the sternum (fig. 25 A, H, L, M, *Cxpd*), consisting of a median area (*c*) and often a pair of lateral stylus-bearing lobes (H, *b*). It is suggestive, therefore, that the stylus-bearing plate, or *styliger*, is a product of the united coxopodites. If so, the lateral parts of the styliger may become secondarily completely separated from the median part (I, J, *c*), forming a pair of distinct stylus-bearing lobes (*b*) containing the stylus muscles. This last condition, well shown in *Ephoron leukon* (J), might therefore be taken as primitive, and the evidence would then seem to show that the styliger has been evolved by the union of a median part of the sternum with the coxopodites (J, I, H, G), and separated from the rest of the sternum as a stylus-bearing plate movable on the latter. The principal weakness of this second view is that it does not account for the original presence of the muscles that move the styliger (A, G, *cxmcl*), which according to the first view are assumed to be sternocoxal muscles. The development of the claspers sheds no light on the morphology of the organs. As shown by Speith (1933) the

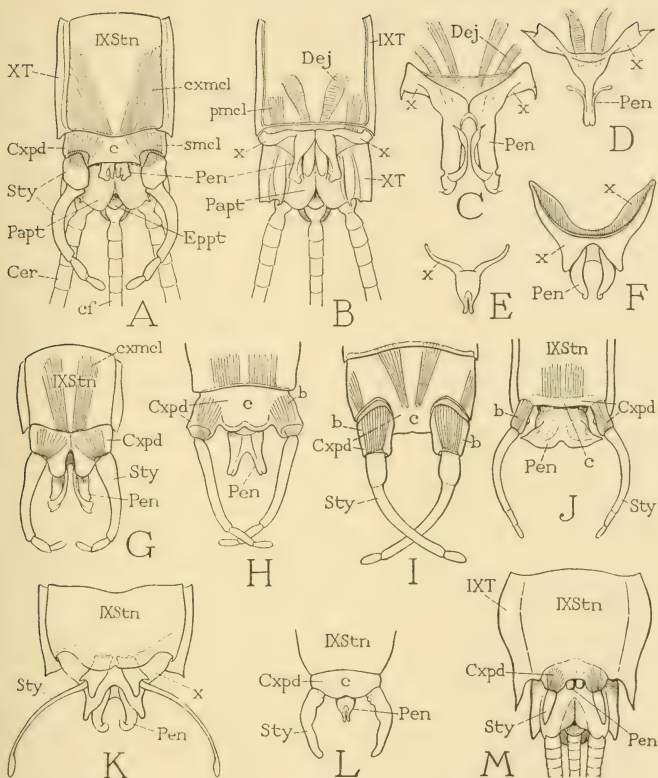


FIG. 25.—Hexapoda-Ephemeroptera: external male genitalia and associated structures.

A, *Ephemera similans*, posterior part of abdomen, ventral view. B, same, styli and stylus-bearing plate removed, exposing bases of penes and supporting arms. C, *Blasturus nebulosus*, penes, ventral view. D, *Habrophlebiodes bettoni*, penis, ventral view. E, *Trichorythodes fallax*, penis, ventral view. F, *Campsurus decoloratus*, penes and basal plate, dorsal view. G, *Blasturus nebulosus*, ninth abdominal segment with styli and penes, ventral view. H, *Iron humeralis*, end of ninth abdominal sternum with styli and penes, ventral view. I, *Bactis vagans*, ninth abdominal sternum and styli, ventral view. J, *Ephoron leukon*, ninth abdominal sternum with styli and penis, ventral view. K, *Campsurus decoloratus*, ninth abdominal segment with styli and penes, ventral view. L, *Trichorythodes fallax*, ninth sternum with styli and penis, ventral view. M, *Onicigaster distans*, larva, posterior part of abdomen, ventral view.

b, stylus-bearing lobe of styliger (united coxopodites); c, median part of styliger; Cer, cercus; cf, caudal filament; cxmcl, muscles of coxopodite arising on ninth abdominal sternum; Cxp, coxopodite; Dej, ductus ejaculatorius; Eppt, epiproct; IXStn, ninth abdominal sternum; Papt, paraproct; Pen, penis; pmcl, muscles of basal arms of penis arising on ninth sternum; smcl, muscles of stylus arising in coxopodite; Sty, stylus; x, basal arms or supporting plate of penes; XT, tenth abdominal tergum.

styliger plate is present in the larva (fig. 25 M), where, though it may differ in size and shape from that of the adult, it is already separate from the ninth sternum and gives origin to the stylus muscles.

The styli are slender appendages varying somewhat in relative length and thickness in different species. They are commonly jointed, i. e., subdivided into several parts called "segments", but the joints are often mere constrictions, and the intervening parts are not true segments since they are never muscled. Usually each stylus has three subsegments (fig. 25 G-J, L), but in some cases there are four (A), in others only two (K), and in the genus *Caenis* the styli are undivided. The larval styli may be simple unjointed processes (M, *Sty*), or they may be subdivided, but, according to Speith (1933), the number of parts is always less than that in the adult stylus of the same species. The basal part of the stylus in some cases might be confused with the coxopodite, or vice versa (A, I, J), and it is only by an examination of the musculature that the two parts of the appendage can be certainly identified: the stylus muscles always take their origin in the coxopodite, whether the muscle-containing part of the latter is a free lobe (I, J) or a part of the styliger plate (A, H).

The posterior position of the mayfly claspers on the ninth abdominal segment may be difficult to reconcile with the idea that the styli are serial homologues of the laterally placed gills of the more anterior segments in the larva (see Snodgrass, 1931), and yet the evidence is equally strong (or weak) in each case that the organ in question is a derivative of a segmental appendage. Perhaps the truth is that some of our ideas about insect morphology are not to be taken too seriously, but in their favor it may be said that, where inconsistencies are not too inconsistent, they establish a fundamental concept on which may be based a uniform terminology. The simple form of the genital appendages in certain larval Ephemeroptera (fig. 25 M) connects these organs with the styli of Thysanura and Orthoptera, and there can be little doubt that the ephemerid styli, on the other hand, represent the movable genital claspers of higher insects, though in the latter the organs seldom have a styluslike form. It is tempting to regard the abdominal stylus in any case as the telopodite of a simplified appendage—the only objection to so doing is the presence of a similar coxal stylus on the thoracic legs of *Machilis* in addition to the true telopodite.

The penes of the mayflies vary in shape and relative size in different species (fig. 25 B-H, J, K, *Pen*) and are often provided with accessory processes (C, D). They may be united with each other in varying degrees (D, E, H), but there are always two ejaculatory



ducts with separate orifices. The two penes are supported either on a pair of divergent basal arms (B, C, D, E,  $x$ ), or on a common basal plate (F, K,  $x$ ) with lateral prolongations. The ends of the basal arms are always intercalated between the adjacent lower angles of the tergal plates of the ninth and tenth abdominal segments (B,  $x$ ,  $x$ ), in some forms they are more closely attached to the ninth tergum, in others to the tenth. The supporting structure of the penes is usually concealed above the stylicher plate, and is implanted on a mem-

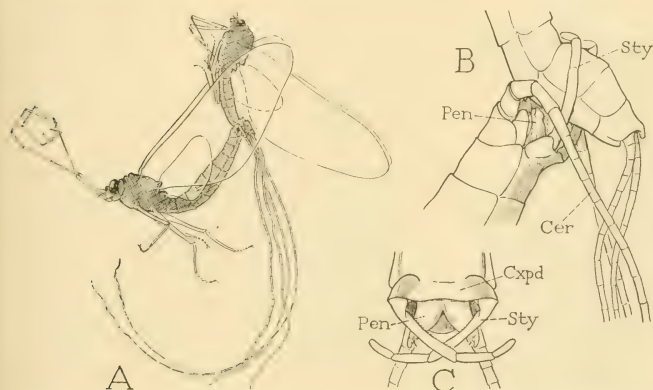


FIG. 26.—Ephemeroptera: copulation and external male genitalia of *Cinygmula minus*.

A, male and female in copulation (drawn from a slide mount loaned by Dr. J. G. Needham). In life probably the body of the female is more nearly parallel with that of the male, and her thorax held in the loop of the long front tarsi of the male. B, the copulating parts of same, more enlarged, showing the use of the styli as claspers. C, end of male abdomen, ventral view.

*Cer*, cerci; *Cxp*, coxopodite plate, or stylicher; *Pen*, penis; *Sty*, stylus.

branous area or fold between the ninth sternum in front and the paraprocts behind (B). There is thus no part of the venter of the male abdomen that can be referred to the tenth segment unless it is the basal plate or arms of the penes and the supporting membrane. Considering the evidence (see page 58) that the primary gonoducts of male insects opened on the tenth abdominal segment, it is consistent to suppose that the primitive paired penes were processes of the sternum or of the appendage bases of this segment. The paired penes of the Ephemeroptera, being evidently primitive organs, should therefore belong to the tenth abdominal segment, and the forward



extension of the paraprocts between the lower edges of the tenth tergum (B, *Papt*) suggests that the sternum of the tenth segment has been correspondingly displaced forward. The penes have the same position in larval mayflies (M, *Pen*) as in the adult, but the accessory structures are only weakly developed in the larva. Concerning the development of the penes in Ephemeroptera, Palmén (1884) says the larval vasa deferentia become attached to the body wall at the posterior border of the ninth segment, and at the points of attachment the penis rudiments grow out carrying with them the ends of the ducts.

The writer is indebted to Dr. Jay R. Traver, of Cornell University, for named specimens amply representing the principal variations in the male organs of Ephemeroptera, on which the preceding descriptions are based.

#### DERMAPTERA

Among the Dermaptera there appear to be retained the same two primitive features of the reproductive system found in the Ephemeroptera, namely, the location of the female genital opening immediately behind the seventh abdominal sternum, and the independence of the male exit ducts, which may open separately on a pair of penes. The lateral oviducts of female Dermaptera, however, come together in a short median oviductus communis, while in the male the independence of the gonoducts is never as complete as in the Ephemeroptera, and the paired penes are united upon a common basal plate that forms a large flat apodeme for muscle attachments. In many forms, moreover, the intromittent organ is a single penis with either a pair of outlet ducts, or a single complete duct. The external genitalia of Dermaptera have been described by Meinert (1868), Jordan (1909), Heymons (1912), Zacher (1911), Burr (1915, 1916), Crampton (1918), Walker (1922), Snodgrass (1935).

A dermapteran intromittent organ of the double type occurs only in the Labiduroidea. The two penes here present are concealed in a deep genital chamber above the long ninth abdominal sternum. Their bases arise close together (fig. 27 A) from the anterior wall of the genital chamber (*x-x*) where they are united upon a common apodemal plate (*Ap*) extending forward. Each penis (*Pen*) consists of a basal stalk bearing two distal lobes, and is traversed by a ductus ejaculatorius (*Dej*). The median lobe (*a*) is the true terminus of the penis and contains an eversible end-sac (preputial sac, *c*), into which the ejaculatory duct discharges; the lateral lobe (*b*) is an accessory process, or paramere, of the penis. A long slender rod, or virga, usually accompanies each ejaculatory duct, its apical part being pro-

tracted with the eversion of the end-sac. The ductus ejaculatorii, though independent for some distance before entering the penes, are united anteriorly in a ductus conjunctus (*Dejcn*), which takes its origin in a saclike seminal reservoir (*rs*) that receives the two vasa deferentia (*Vd*).

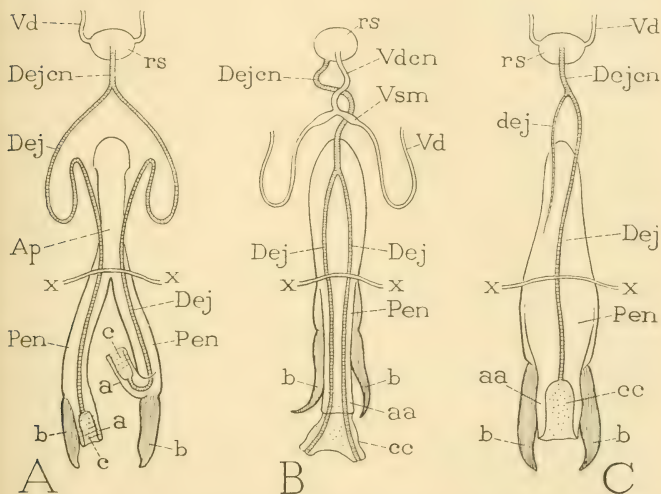


FIG. 27.—Hexapoda—Dermaptera: three types of structure in the male genital exit system and the intromittent organ. (Diagrams based on Meinert, 1864, 1868; Jordan, 1909; Heymons, 1912; Walker, 1922; Snodgrass, 1935.)

A, Labiduroidea, penes separate beyond common basal apodeme. B, *Hemimerus talpoides*, penes united, but both exit ducts retained. C, Forficuloidea, penes united, only one functional duct.

*a*, median lobe of penis; *aa*, median lobe of conjoined penes; *Ap*, basal apodemal plate of penes or penis; *b*, paramere lobe of penis; *c*, eversible end-sac of penis; *cc*, end-sac of conjoined penes; *Dej*, ductus ejaculatorius; *dej*, nonfunctional branch of ejaculatory duct; *Dejcn*, ductus ejaculatorius conjunctus; *Pen*, penis; *rs*, seminal reservoir; *Vd*, vas deferens; *Vdcn*, vas deferens conjunctum; *Vsm*, vesicula seminalis; *x-x*, anterior wall of genital chamber.

In *Hemimerus* and Forficuloidea the penis is a single structure (fig. 27 B, C), but, since it is armed with two paramere processes (*b*, *b*) arising at the sides of a median terminal lobe (*aa*) containing an eversible end-sac (*cc*), there can be no doubt that the organ has been produced by the union of two penes having the structure of the paired organs of Labiduroidea (A). Two ductus ejaculatorii traverse the penis of *Hemimerus talpoides* (B, *Dej*), but they fork in

the base of the penis from a ductus conjunctus (*Dejcn*) that proceeds from a seminal reservoir (*rs*), into which the vasa deferentia discharge by a common duct (*Vdcn*) after first enlarging as a pair of seminal vesicles (see Jordan, 1909, Heymons, 1912). The two exit ducts of *Hemimerus* open separately into the end-sac of the penis, which is shown everted in the diagram (B, *cc*). In *Forficula* (C), as described by Meinert (1864) and by Walker (1922), the vasa deferentia discharge separately into the seminal reservoir, and a single outlet duct (*Dejcn*) proceeds posteriorly from the latter but soon divides into two branches; one branch (*dej*), however, is rudimentary and has no distal connection, the other (*Dej*) traverses the penis as the functional duct and opens into the eversible end-sac (*cc*).

The presence of a rudimentary ejaculatory duct in the Forficuloidea leaves little doubt that the structure of the male organs in Labiduroidea (fig. 27 A) represents the more generalized condition in the Dermaptera, and that the imperfectly unified organs of the other groups (B, C) have been derived from completely paired structures. In *Hemimerus* the terminal parts of both exit ducts remain functional in association with a penis conjunctus; in Forficuloidea one duct is functionally suppressed. This manner of transition within the Dermaptera from paired penes with individual exit ducts to a single intromittent organ with one functional duct might be supposed to show the method by which the median penis (phallus) and single exit apparatus of other male insects has been evolved. There is, however, no specific evidence of the production of a median intromittent organ by the union of paired penes in any insects other than Dermaptera and Ephemeroptera, and in these two orders a union of the penes has taken place quite independently. Moreover, the ontogenetic development of the common ductus ejaculatorius of other insects shows that this duct, from its inception, is an independent median ingrowth of the ectoderm, and suggests that it probably originated phylogenetically as an invagination of the body wall at the approximated mouths of the lateral ducts, as it does in the ontogeny of Thysanura.

#### PLECOPTERA

The Plecoptera in some respects may present a fairly generalized condition of the specialized organization of the wing-flexing group of pterygote insects; but the male reproductive organs are in no way generalized, and they furnish no lead toward the evolution of the genitalia in higher insects. In fact, the structures that form the basis for most of the elaboration in the external genital mechanism of

other insects are either reduced or suppressed in both sexes of the stoneflies. In the female the gonotreme, or vulva, lies above the posterior margin of the eighth abdominal segment (fig. 29 C, *Gtr*), where it opens from a small genital chamber containing the oviducal and spermathecal apertures; but an ovipositor is entirely absent. The two small processes borne by the eighth sternum in females of *Pteronarcys* are clearly not true gonapophyses, since the latter always arise posterior to the sternal plate. In some forms the lateral oviducts appear to discharge separately into the genital chamber (vagina), in others they first unite with a very short oviductus communis (see Klapálek, 1896; Mertens, 1923; Wu, 1923). The genital segments of the male have no appendicular organs that can be referred to segmental limbs, comparable with the styli of apterygote insects, Ephemera, and Orthoptera, or with the movable claspers (harpagones) of other Pterygota. The functional intromittent organ is in most cases a phallic structure, though a median process of the epiproct has been described as a "sperm conveyor", and in the genus *Leuctra* it is possible that a pair of ventral processes of the tenth segment conduct the sperm to the female from the male genital opening situated at their bases. In the families Pteronarcidae and Perlidae the "penis" is principally a large, eversible endophallic sac, accompanied or not by an ectophallus; in the other families, Nemouridae and Capniidae, there may be present a short tubular ectophallus, which contains the opening of the genital exit passage, but the latter has not been shown to be eversible. The occurrence of "paired penes" has been claimed, but not demonstrated. Whatever accessory genital structures are present in the Plecoptera are secondary processes, usually of the tenth and eleventh abdominal segments, but also of the eighth and ninth. Information on the exact function of the phallic organs and accessory genital processes in the order is far from complete.

The internal reproductive organs of the Plecoptera are highly variable in the several families, particularly with respect to the grouping of the testicular tubules, and in the size and character of the median exit duct. The testes have no peritoneal investiture, the sperm tubes being free from one another, as are the egg tubes of the ovaries, and, so far as noted, the gonads have no suspensory ligaments in either sex. Only in the genus *Leuctra* (Nemouridae) have the vasa deferentia been described as being independent of each other (Klapálek, 1896; Mertens, 1923); in such cases the testes consist of groups of slender tubules arising from the anterior ends of the ducts (fig. 28 A, *Tes*). In other forms the vasa deferentia of opposite sides are united; in some cases they have coalesced for a considerable length

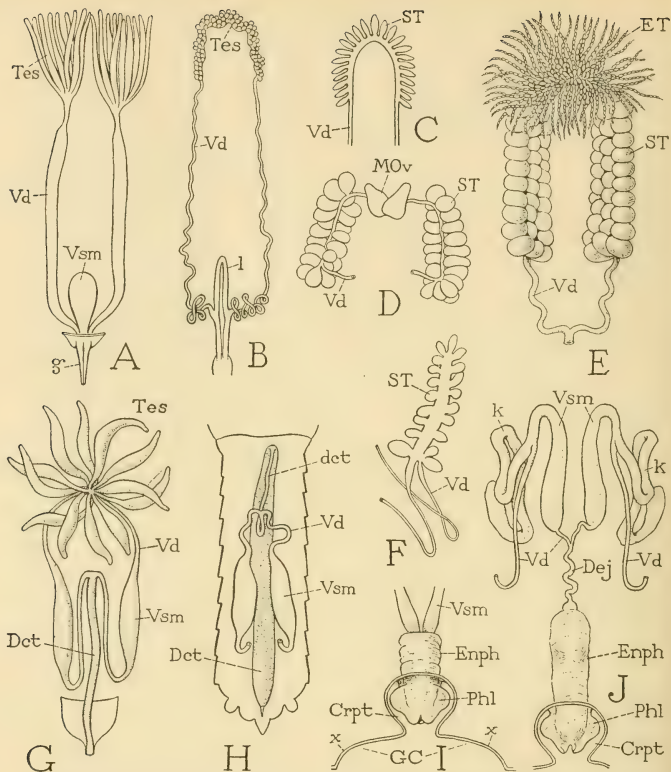


FIG. 28.—Hexapoda—Plecoptera: internal male reproductive organs. (A, B, C, and F from Klapálek, 1896; D from Junker, 1923; E from Schoenemund, 1912; G from Mertens, 1923; H from Wu, 1923.)

A, *Leuctra nigra*, testes in terminal groups at ends of vasa deferentia, median exit duct very short. B, *Perlodes* (*Dictyoptyerix*) *microcephala*, vasa deferentia united anteriorly in arch bearing numerous sperm tubes, connected posteriorly by looped commissure (I). C, *Taeniopteryx trifasciata*, sperm tubes in series on united anterior parts of vasa deferentia. D, *Perla marginata*, male larva 12 mm long, immature testes with "male ovaries" (MOv) and sac-like sperm tubes (ST). E, same, older larva, with numerous egg tubes (ET) on anterior arch of vasa deferentia. F, *Capnia nigra*, single testis formed by lengthwise union of parts of vasa deferentia bearing sperm tubes. G, *Protonemoura praecox*, sperm tubes grouped at union of vasa deferentia, the latter discharge directly into long median exit duct. H, *Nemoura vallicularia*, vasa deferentia discharge into slender median duct (dct), which opens into large terminal exit duct (Dct). I, *Acroncuria arida*, median genital exit apparatus as seen in undisturbed dissection. J, same, parts of exit apparatus artificially extended.

Crpt, phallocrypt; Dct, large median exit duct; dct, small median exit duct; Dej, ductus ejaculatorius; Enph, endophallus; ET, egg tube; g, genital process of tenth sternum (see fig. 29, M); GC, genital chamber; k, diverticula of vasa deferentia; I, commissure between vasa deferentia; MOv, "male ovaries"; ST, sperm tube; Tes, testis; Vd, vas deferens; Vsm, vesicula seminalis; x-x, inner wall of genital chamber.



of their anterior parts (F), in others they are continuous end to end in an arch over the alimentary canal (B, C, D, E, G). The sperm tubes of the united ducts are either distributed along the lateral or anterior parts of the ducts (B, C, D, E), or they are clustered at the point of union (G). The various types of male organs found in the order are described and illustrated by Klapálek (1896) and Mertens (1923), and a more detailed account of their structure is given by Schoenemund (1912) for species of *Perla*, and by Wu (1923) for *Nemoura vallicularia*. In the male of *Perla marginata*, in which the united vasa deferentia form a large loop from one side to the other, the gonadial tubes of the anterior part of the arch, as shown by Schoenemund (fig. 28 E), during a late larval stage take on the form of small ovarioles (ET) and contain egglike cells, while those of the lateral parts form large oval testicular sacs (ST) in which the spermatozoa are developed. Each male ovariole, according to Schoenemund (1912) and Junker (1923), has the structure of a typical panoistic egg tube with a series of 12 to 18 oocytes enclosed individually in cellular follicles. At an earlier larval stage, Junker observed, the egg tubes are enclosed in a pair of ovarian sacs, or "male ovaries" (D, MOv), situated on the median part of the arch of the duct, but he says a few oocytes are to be found also in the saclike sperm tubes (ST). The "male eggs" of *Perla marginata*, however, were found by Junker to possess the diploid chromosomes of the spermatid cells; they never complete normal maturation, and the tubules containing them degenerate at the transformation to the adult.

The vasa deferentia are generally enlarged toward their posterior ends to form storage vesicles for the spermatozoa (fig. 28 A, G, H, J, Vsm). In some forms a tubular diverticulum (J, k) is given off from each duct. Klapálek describes a condition in species of several genera in which the two ducts are connected by a transverse vessel (B, l) looped forward between them, which he regards as a vesicula seminalis. In *Leuctra*, according to Klapálek and Mertens, a sperm vesicle in the form of a median pouch arises at the junction of the vasa deferentia with the ejaculatory duct (A, Vsm).

The median genital exit system of male Plecoptera varies considerably among different genera in the relative development of its parts, and the identities of the latter are difficult to follow in published descriptions of the genital organs. In a freshly dissected specimen of *Acroneuria* (fig. 28 I) the two tubular vesiculae seminales (Vsm) appear to discharge directly into a large sac (Enph) opening through the ectophallus (Phl); but if the parts are pulled out lengthwise (J) it is seen that there are short terminal sections of the vasa



deferentia beyond the vesiculae, which unite in a slender ductus ejaculatorius (*Dej*), and that the latter opens into the anterior end of the phallic sac (*Enph*). There can be no question in this species that the terminal sac of the exit system is an endophallic invagination from the mouth of the external penis, or ectophallus (*Phl*). The endophallus is everted during copulation (fig. 29 E, *Pen*), and in the protracted condition it forms the principal part of the intromittent organ. The everted "penis" of *Acroncuria pacifica* is figured by Needham and Claassen (1925), that of *Acroncuria evoluta* by Clark (1934). Other species shown to have an eversible phallic organ include *Pteronarcys nobilis* (Frison, 1935), *Perla hastata*, *Perlodes signatus*, and *Isoperla fusca* (Needham and Claassen, 1925). The wide exit tube of *Chloroperla grammatica* and of *Isopteryx tripunctata* described by Klapálek (1896) as the "ductus ejaculatorius" is very evidently an eversible structure. An eversible endophallus, therefore, is probably a characteristic feature of the families Pteronarcidae and Perlidae.

The walls of the endophallus are mostly membranous, but they may contain sclerotic areas or plates, and in some forms they are produced into folds or are armed with a pair of long rods or hooklike processes, all such structures taking an external position with the eversion of the sac. The exposed rods or hooks are called "titillators" by most writers, but a rodlike internal armature of the endophallus is generally termed a *virga* (fig. 22 B, *Vrg*), and the name *titillator* given to terminal processes of the ectophallus (*Ttl*).

The endophallus may be a direct invagination from the anterior wall of the genital chamber, as shown by Klapálek in *Chloroperla* (*Isopteryx*) *tripunctata*, in which the long tube, designated "ductus ejaculatorius" by Klapálek, opens simply by a wide mouth, from which project the tips of the endophallic rods, or virgae. In other Perlidae, however, an ectophallus may be present as a distinct "penis" projecting into the genital chamber and containing the mouth of the endophallus. An organ of this type is well shown by Walker (1922) in *Perla tristis* as a large globular structure concealed in the genital chamber above the ninth abdominal sternum. In *Acroncuria arida* (fig. 28 I, J) the ectophallus (*Phl*) is a thick, conical lobe somewhat constricted at its base, with an apical opening that leads into the wide endophallic sac (*Enph*). The phallus of this species, however, is not seen directly on opening the shallow genital chamber; it is concealed in a deep pocket (phallocrypt, *Crpt*) of the genital chamber wall, the aperture of which appears at the bottom of the external cavity. The

fully everted "penis" in this case includes the endophallus, the ectophallus, the phallocrypt, and probably also the shallow genital chamber.

In the families Nemouridae and Capniidae there appears to be no evidence that the functional intromittent organ is an everted structure. The median exit duct is in some cases short and in others long, and, in species studied, it terminates in an ectophallus, which, however, may be very small. The terminal exit duct of *Nemoura vallicularia*, as shown by Wu (1923), is a long median tube extending forward almost to the base of the abdomen (fig. 28 H, *Dct*); it is enclosed in a thick sheath of strong muscular fibers, and ends in a short, tapering sclerotic penis. Opening into the anterior end of this tube, however, is a much slenderer median duct (*dct*) that receives the two vasa deferentia, as in *Acroneuria* (J, *Dej*). We might suspect, therefore, that the large duct of *Nemoura* is a noneversible endophallus, and that the slender duct is the true ductus ejaculatorius. The internal genital structures of *Protonemoura praecox*, as described by Mertens (1923), are the same as those of *Nemoura vallicularia* except that here the vasa deferentia discharge directly into the large median tube, which latter Mertens says has extraordinarily strong muscular walls and evidently serves to expel the spermatid fluid. A similar, strongly muscular exit passage is present in *Taeniopteryx maura* and opens through a wide, bluntly conical ectophallus. The latter is protracted in one specimen observed, but there is no accompanying eversion of the duct. Wu (1923) describes the development of the exit duct in *Nemoura* from an invagination of the body wall between the ninth and tenth abdominal sterna, beginning with the ninth instar and increasing in length during subsequent instars. In the earlier stages the vasa deferentia open directly into the median tube, which thus appears in its inception to be the ductus ejaculatorius. A "diphallid" condition is said by Crampton (1918) to occur in *Nemoura completa*, but since the structures designated "penes" are not demonstrated to be such by dissection, we may suspect that they are merely phallic lobes, and that a single genital orifice will be found between them.

In the genus *Leuctra* the phallic apparatus is much reduced, and it appears that the intromittent function may be performed by a pair of processes arising from the sternum of the tenth abdominal segment. These structures are described by Klapálek in *L. nigra* and *cylindrica*, and by Mertens in *L. prima* and *hippopus* as a pair of sclerotic processes (Chitingräten, Titillatoren) arising at the sides of the genital orifice, and embraced by two prolongations of the plates of the tenth sternum. Each median process, according to these authors, is

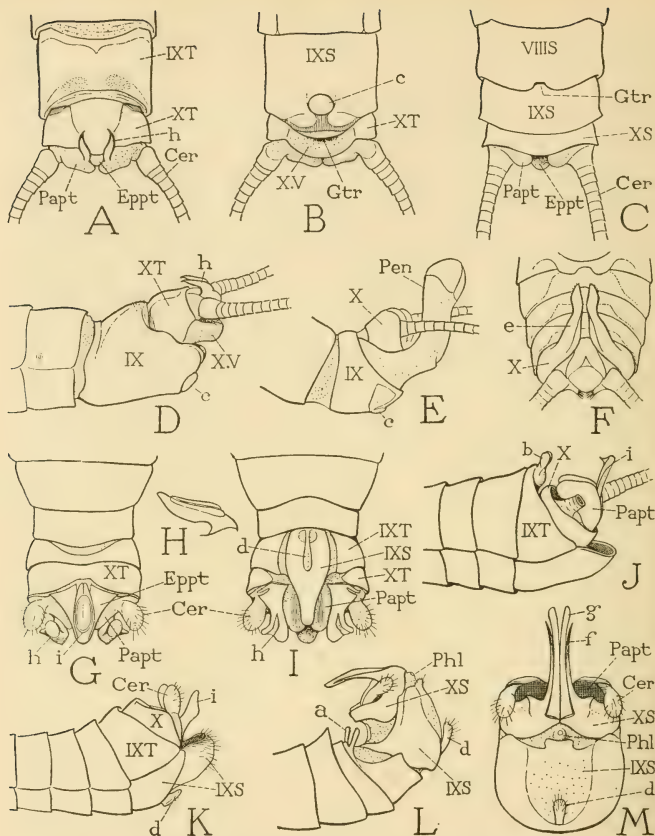


FIG. 29.—Hexapoda-Plecoptera: external genitalia.

A, *Acroneuria arida*, male, end of abdomen, dorsal view. B, same, ventral view. C, *Acroneuria*, female, end of abdomen, ventral view. D, *Acroneuria arida*, male, end of abdomen, lateral view. E, *Acroneuria evoluta*, end of abdomen with protracted penis (from Clark, 1934). F, *Neophasganophora capitata*, end of abdomen, dorsal view (from Frison, 1935). G, *Nemoura bifurcata*, end of abdomen, dorsal view. H, same, supra-anal process, lateral view. I, same, end of abdomen, ventral view. J, *Pteronarcys proteus*, end of abdomen, lateral view. K, *Taeniopteryx maura*, end of abdomen, lateral view. L, *Leuctra sibleyi*, end of abdomen, lateral view. M, same, ninth and tenth abdominal segments, ventral view.

a, tergal process of eighth abdominal segment; b, tergal process of ninth segment; c, percussion disc of ninth sternum; Cer, cercus; d, basal lobe of ninth sternum; e, lateral process of tenth segment; Eppt, epiproct; f, g, lateral and median ventral processes of tenth sternum; Gtr, gonotreme (opening of genital chamber); h, dorsal process of paraprot; i, median process of epiproct; IX, ninth abdominal segment; Papt, paraprot; Pen, penis (protracted phallic organs); Phl, ectophallus; S, sternum; T, tergium; X, tenth abdominal segment; XV, membranous venter of tenth segment.

grooved on its inner surface, the two apposed processes thus forming a channel through which the spermatic fluid is conveyed from the ejaculatory duct. The four processes are well developed in *Leuctra sibleyi* (fig. 29 M, *f*, *g*), in which collectively they appear as a large arm projecting anteriorly above the end of the abdomen from the up-turned sternum of the tenth segment (L). The longer median processes (M, *g*) are flattened and slightly concave on their apposed faces, and are movably attached at their bases in notches of the tenth sternal plates (XS). The slenderer, tapering lateral processes (*f*) are direct continuations of the sternal plates, but, owing to a partial membranization of the latter, they can be turned outward by sternal muscles inserted laterad of their bases. The genital opening of *L. sibleyi* appears to be on a small phallic papilla (L, M, *Phl*) in the membranous area between the ninth and tenth abdominal sterna at a point where the discharged sperm might enter the channel between the sternal processes of the tenth segment. The median exit duct is shown by Klapálek and by Mertens to be very short in species of *Leuctra* (fig. 28 A), with a median stalked "vesicula seminalis" arising from it at the junction with the vasa deferentia.

The external genital armature of male Plecoptera consists of secondary outgrowths or lobes of the posterior abdominal segments. Though some of these structures are movable by a special adaptation of the segmental muscles, it is clear that none of them represents the styli of the apterygote insects and Orthoptera, or the stylus derivatives in the form of independently muscled claspers, or harpagones, of the Ephemera and higher insects, which so commonly are the most important features of the periphallid genitalia. In the evolution of the Plecoptera, therefore, the usual accessory genital structures, including the ovipositor of the female, have been discarded, and in the male there has been developed a profusion of secondary structures.

The principal accessory genital developments of male stoneflies pertain to the tenth and eleventh abdominal segments, but lesser structures occur frequently on the ninth segment, and sometimes on the eighth. Among the species here illustrated, examples of tergal processes on the eighth and ninth segments are seen in *Leuctra sibleyi* (fig. 29 L, *a*) and in *Pteronarcys proteus* (J, *b*). In *Acroneuria* the ninth sternum bears a smooth round or oval elevation near its posterior margin (B, D, E, *c*) known as the percussion disc, or hammer, with which the male is said to make a drumming sound by tapping on the surface beneath him (see Macnamara, 1926). Most of the Nemouridae have a small elongate ventral lobe flexibly attached to the base of the ninth sternum (I, K, L, M, *d*). The posterior margin

of the ninth sternum may form but a rounded lip beneath the genital opening, or gonotreme, above it (B), or it may be produced into a subgenital lobe of varying length (I, K, M), which in some forms is differentiated from the rest of the sternum by a weaker sclerotization (K).

The tenth segment is always a distinct annulus, though it varies in form and size and in the relative development of its sclerotized areas. In some species the tergum of the tenth segment is a large plate covering the back and sides (fig. 29, A, D, G, XT), whereas the venter is unsclerotized (B, D, I) and may appear as a membranous fold behind the gonotreme (B, XV). In others the reverse occurs, a large sternal plate being the principal sclerite of the tenth segment (L, M, XS); or again, both the tergum and the sternum may be confluent in a continuously sclerotized ring (J, K, X). The armature of the tenth segment consists most commonly of lateral lobes or hooklike processes produced upward from the posterior margins (F, e); but in *Luctra*, as already described, the sternum of the segment bears a group of processes arising just behind the genital orifice (M, f, g). By the upward curvature of the end of the abdomen the tenth segment may be inverted (L, XS), and the sternal processes then project dorsally and anteriorly. In some forms a short process arises from the posterior margin of the tenth sternum.

The eleventh segment consists of the usual epiproct and paraprocts (fig. 29 A, *Eppt*, *Papt*), with the cerci (*Cer*) arising at the bases of the latter. The cerci are typically long, slender, multiarticulate appendages, but in the Nemouridae they are reduced, those of the male in most cases consisting of a single "segment" (G, I, K, L, M, *Cer*). The armature of the eleventh segment includes a pair of processes borne by the paraprocts, and a median process of the epiproct, though either or both may be absent. The paraproctial processes arise from the upper surfaces of the paraprocts and project dorsally. They commonly have the form of a pair of hooks (A, D, h), but they may take on more complex shapes (G, I, h). They are said to be used by the male for depressing the subgenital plate of the female. In the mating position the male rests upon the back of the female, and, in the manner of a grasshopper, lowers his abdomen on one side of that of the female and turns the end upward beneath the genital region of the female (see description by Hagen, 1877, figure by Wu, 1923). The everted or protracted phallus projects upward and forward, its end presumably being inserted into the female genital chamber.

The median process of the epiproct is variously developed, often attaining a large size and complex structure (fig. 29 G, J, K, i). It



has been fully described in *Pteronarcys* by Hagen (1877) and by Smith (1917). The organ usually projects dorsally or forward from the end of the epiproct, and may be grooved lengthwise on its posterior surface. It was first described by Hagen as a "penis" in the sense of being an organ for conducting the sperm from the genital aperture of the male to that of the female, a function which Hagen claimed to have proved by observation, and the organ has since been known generally as the "sperm conveyor." In *Nemoura vallicularia*, however, Wu (1923) observes that the supra-anal process serves merely to support the ninth segment of the female during mating, and Needham and Claassen (1925) describe the organ of *Perlodes signatus* as a guide for "the large soft penis that issues from the apex of the ninth segment beneath." Hagen and Smith apparently did not observe the eversible penis in *Pteronarcys*, which has been shown by Frison (1935) to be present and protractile in this genus.

For a more extensive comparative study of the external genital structures of male Plecoptera the student should consult the works of Klapálek (1896), Smith (1917), Crampton (1918), Walker (1922), Needham and Claassen (1925), and Frison (1935).

#### ORTHOPTERA

As this paper was originally planned, the Orthoptera were to occupy a prominent place in it, because it was supposed that, considering the antiquity of the Orthoptera in hexapod chronology, the structure and development of the external genital organs of the male would give evidence of the nature of the primitive phallic organs of insects in general. More familiarity with the subject, however, now suggests that the complex phallic structures of the various orthopteroid families have been evolved within the order; there is no evidence that in their origin these structures have been developed from paired penes, and in their evolution certainly they have not produced an organ comparable with the phallus of other insects.

The male genitalia of Blattidae consist essentially of three phallic lobes arising from the anterior wall of the genital chamber close to the opening of the ejaculatory duct. Two of these lobes, or phallomeres, are right and left with respect to the gonopore, the third is ventral. In young nymphs the phallomeres are simple lobes of small size, but with each ecdysis the lateral lobes increase in size and present an altered or more complex structure. In the adults of some forms (*Blatta*, *Periplaneta*) the right and left phallomeres (parameres of Walker, 1922) become large organs subdivided into many parts



and provided with an elaborate musculature, while the ventral phallomere takes the shape of a broad lobe with the gonopore on its base. In others (*Blattella*, *Ectobia*) the lateral phallomeres retain a relatively simple form, and become retracted into pouches of the genital chamber laterad of the gonopore, while the ventral lobe forms the mouth of a large endophallic sac receiving the ductus ejaculatorius into its anterior end, and having a long rod, or virga, in its dorsal wall. The exact use of the phallic organs of Blattidae during mating has not been observed, and apparently it is not known in what manner the spermatozoa are transferred to the female seminal receptacle. In *Blatta orientalis* the spermatozoa occur within the receptacle attached externally to long tubular spermatophores.

In Tettigoniidae and Gryllidae a phallic organ is variously developed, including ectophallic and endophallic parts, but there is no close resemblance in any case to the genital structures of Blattidae, and there is little in the ontogeny of the organ to indicate that the adult structures have been evolved from any type of primitive structure common to the Orthoptera. The principal modifications of the phallus in the Tettigoniidae and Gryllidae are adaptations to the formation of spermatophores and the introduction of the latter into the genital chamber or the spermathecal orifice of the female; the phallic mechanism is fairly well understood in most cases. The complex phallic organ of Acrididae is perhaps an extreme development of the tettigoniid type of structure, in which a large endophallic cavity becomes an important part of the phallic apparatus.

The Male Genitalia of Orthoptera will be the subject of a separate paper designed to follow, in which will be discussed the structure and function of the male organs in orthopteroid families other than Acrididae.

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SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 15

Arthur Fund

FURTHER EVIDENCE ON  
THE DEPENDENCE OF TERRESTRIAL  
TEMPERATURES ON THE VARIATIONS  
OF SOLAR RADIATION

BY

C. G. ABBOT

Secretary, Smithsonian Institution



(PUBLICATION 3397)

CITY OF WASHINGTON

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AUGUST 12, 1936



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### FURTHER EVIDENCE ON THE DEPENDENCE OF TERRESTRIAL TEMPERATURES ON THE VARIATIONS OF SOLAR RADIATION

By C. G. ABBOT

*Secretary, Smithsonian Institution*

A former paper on this subject<sup>1</sup> showed how the temperatures of Washington, St. Louis, and Helena seem to depend on the rise and fall of solar radiation. Table 1 of that publication gave a series of dates in all months of the year from the year 1924 to 1935 on which the solar radiation apparently began either to rise or to fall for a succession of several days. In figure 2 (here reproduced as figure 1) was shown the opposite average marches of temperature at Washington for 16 days after such opposite changes of solar radiation began.

On the basis of the evidence contained in this paper, Dr. R. A. Millikan composed, and others, including Dr. K. T. Compton, Dr. I. Bowman, and the Chief of the United States Weather Bureau, signed with him, the following memorandum:

The work on solar radiation that has been carried on for a considerable number of years under the leadership of Doctor Charles G. Abbot has apparently brought to light good evidence,

First, that the rate at which radiant energy comes to earth from the sun is not entirely constant but sometimes rises and other times falls through periods of a number of days; and

Second, that these rising or falling periods of solar radiation are followed through as much as sixteen days by measurable temperature variations in the atmosphere as determined by ordinary thermometer readings.

These effects are of so much scientific and practical interest for the problem of predicting at least some elements of the "weather" as much as two weeks ahead that it is our unanimous judgment that there should be not only a continuation of this research but considerable enlargement and refinement of the program, so as to subject these preliminary findings to exceedingly careful and dependable verification and extension.

The Smithsonian Institution has been for at least half a century the agent which has specialized most successfully on solar radiation problems. No other institution is in as good a position as is it to continue to lead in this field. The

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<sup>1</sup> Smithsonian Misc. Coll., vol. 95, no. 12, May 1936.



undersigned therefore, after a most careful study of Dr. Abbot's program, endorse it unreservedly and express the earnest hope that he may receive the appropriations that he needs to make it effective.

An attempt was made to obtain a Federal appropriation of \$200,000 to establish seven additional solar-radiation stations and to undertake

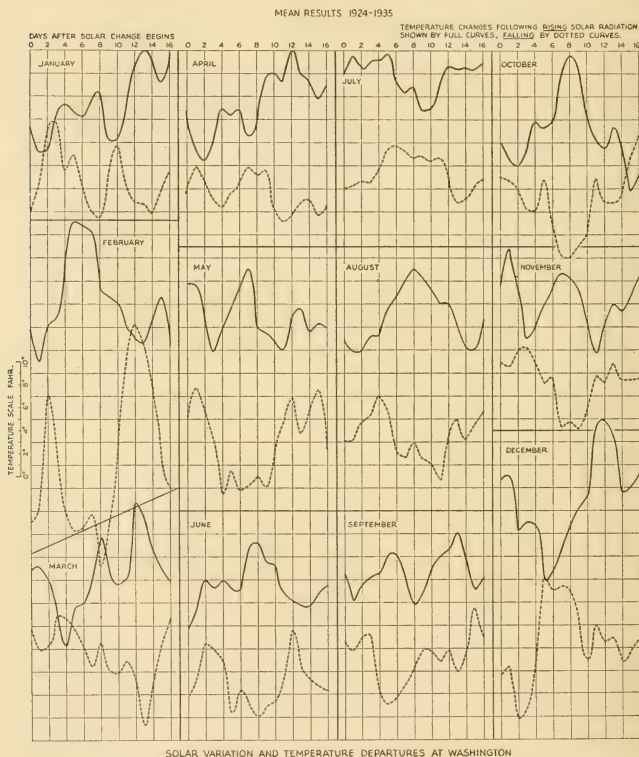


FIG. 1.—Oppositeness of temperature departures at Washington which follow average rising and falling sequences of solar variation.

automatic measures of ultraviolet rays at 100,000-feet altitude. The appropriation passed the Senate but was rejected by the conferees on the urgent deficiency bill. Fortunately, the Smithsonian Institution was able to make a grant of \$5,000 to Dr. Brian O'Brien, of Rochester,

who with the cooperation of the University of Rochester, the Eastman Kodak Co., and other friends will undertake tests of the automatic measurement of ultraviolet solar rays at high altitudes.

In order to more thoroughly buttress the proposition that solar variation is a major factor in the temperature changes of terrestrial

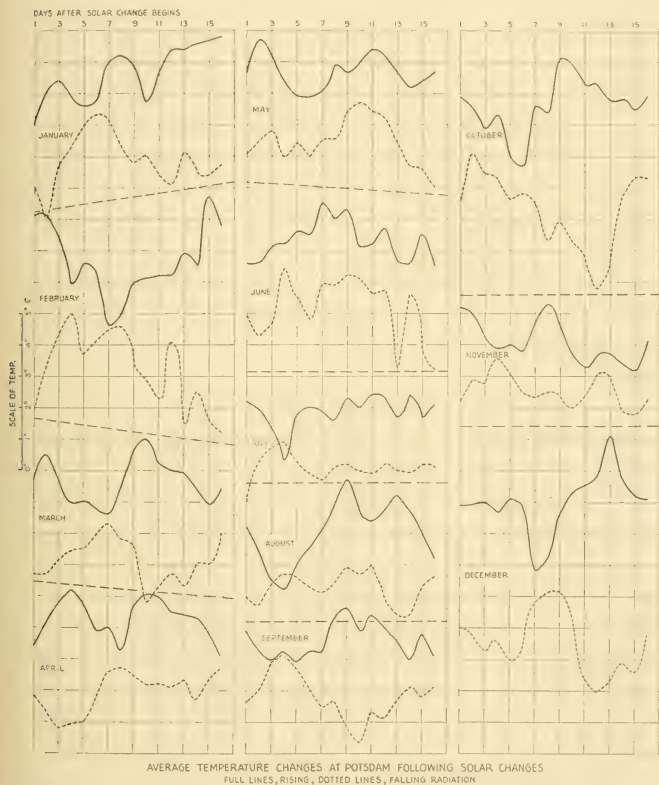


FIG. 2.—Oppositeness of temperature departures at Potsdam which follow average rising and falling sequences of solar variation.

weather, I undertook, with the cooperation of the late C. F. Talman, meteorologist and librarian of the United States Weather Bureau, a study of the weather of Potsdam, Germany, similar to that I made for Washington and other stations. The year 1935 was not available,

but all other dates found in Table 1 of my former publication were used as dates of incipient solar changes.

To obtain departures from approximate daily normals at Potsdam, the values of the daily means of temperature at 7<sup>h</sup>, 14<sup>h</sup>, 21<sup>h</sup> were employed. Monthly means of these daily means were available for the years 1921 to 1934, inclusive.<sup>2</sup> Average monthly values were computed for this interval and plotted on a sufficient scale. A smooth curve was drawn from these monthly averages, and the differences between it and the observed daily mean temperatures were used as temperature departures.

It is recognized that the normals thus obtained are only approximate. But this will not impair the value of the departures for the purpose proposed. For instance, if the normals thus obtained were a little low for a given month, the departures for all years during that month would be prevalingly positive, but the curve of their *fluctuation* over an interval of 16 days would be almost precisely the same as if the normals had been perfect.

Proceeding then in exactly the same way as described in my former publication, cited above, we arrive at the results shown in figure 2. Except for the months of May and June,<sup>3</sup> the results seem to be as emphatically favorable for Potsdam as for Washington to the former conclusions, as follows: Opposite changes of solar radiation are associated for at least 2 weeks after their commencement with opposite marches of temperature departures in weather. These average effects are of the order of several degrees Centigrade, although the solar changes on which they depend are only of the average range of about 0.7 percent. If daily excellent values of the solar constant of radiation, trustworthy to 0.2 percent, were available, certain weather features might probably be predicted for 2 weeks or more in advance. Since theory and observation indicate that the solar radiation changes fractionally perhaps ten times as much near 3,100 angstroms as in the solar constant, there is great hope that automatic records of ultraviolet solar radiation at great altitudes may be of first rate importance for weather forecasting.

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<sup>2</sup> Beob. Obs. Potsdam, Deutsch. Meteorol. Jahrb., Teil 4, Heft 1.

<sup>3</sup> In these two months considerable temperature changes are found at Potsdam, but they run parallel for opposite variations of the sun.

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VOLUME 95, NUMBER 16

A 17<sup>TH</sup> CENTURY LETTER OF GABRIEL DIAZ VARA  
CALDERÓN, BISHOP OF CUBA, DESCRIBING THE  
INDIANS AND INDIAN MISSIONS OF FLORIDA

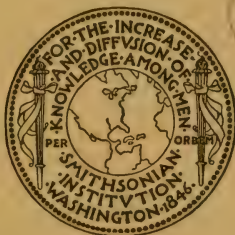
(WITH 12 PLATES)

TRANSCRIBED AND TRANSLATED BY

LUCY L. WENHOLD

Salem College, Winston-Salem, N. C.

INTRODUCTION BY JOHN R. SWANTON



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INTRODUCTION BY JOHN R. SWANTON

The original of the letter described herein is in the Archivo General de Indias at Seville, Spain. Photocopies are owned by the Florida State Historical Society and the North Carolina State Historical Commission, but, in view of its special interest for Floridians, it is hardly less than miraculous that it should have been brought to the attention of scholars through the latter. For this outcome we are especially indebted to Dr. Lucy L. Wenhold, of Salem College, Winston-Salem, N. C., who chanced upon it while examining and transcribing some of the documents of the Commission. From time to time Dr. Wenhold had been kind enough to refer to me such translations as she thought might interest the Bureau of American Ethnology in its work, and this letter happened to be among them.

In the invaluable "List of Documents in Spanish Archives relating to the History of the United States, which have been Printed or of which Transcripts are Preserved in American Libraries", compiled by Dr. James A. Robertson, are cited copies of two other letters by Bishop Calderón, both dated June 8, 1675, and preserved in the Buckingham Smith Collection of the New York State Historical Society. They were written at Havana, one addressed to Juan de Mendoza Escalante, and the other to the Conde de Medellin, of the Council of the Indies. The original of the former is in the Biblioteca Nacional at Madrid, and of the latter in the Archivo General de Indias, Audiencia de Santo Domingo. A third letter written at Havana August 14, 1674, in a hand different from the Bishop's own or that of the accompanying memoir, is of more interest to us because it refers to the visit to

Florida Calderón was about to undertake. Dr. Wenhold translates it as follows:

[The Bishop of Cuba to the Queen]

SEÑORA :

Your Majesty is pleased to command me, in the two royal cédulas of the 4th of March of the year 73, to visit at this time the provinces of Florida and apply the proper remedy in the matter presented to Your Majesty by the Bishop of the city, Rodrigo, my predecessor here. No bishop has gone there [to Florida] in more than 60 years, and the presence of one is needed, not only to celebrate confirmations and correct the faults and abuses that have come in during so long a time in the case of [a] people so recently converted, and to investigate the state in which the priests of San Francisco have the work of converting the Indians and the instruction of the converts under their care, but also to lend encouragement to the converting of the Indians of the province of Apalachocoli who have for years been asking that missionaries be sent to teach and baptize them; a request never yet granted for lack [of missionaries]. In this field the Bishop believes the Dominican priests of this city would accomplish much.

Señora, this my predecessor said to me in the city of San Lucar where I was by order, awaiting the first opportunity of passage to this incumbency. I replied to him that I wished first to come to the city of Cuba,<sup>a</sup> seat of this bishopric, visiting it, and to go then to the mission. Accordingly, as soon as I entered this city, obeying your Majesty I began to plan for the carrying out of that purpose. Having now completed the visitation of this entire island, I have it in such good condition that within 8 days under the favor of God I shall set forth.

And because (although I recognize the great zeal of the Dominican priests, who have offered themselves to me willingly), to take them now would be to introduce great discord with the Franciscans and jeopardize the conversion of those miserable heathen, it has seemed to me wiser to make use of the latter, both because they are well versed in that language and because they are in control of the entire province of Apalache which borders upon that of Apalachocoli. [I go] to investigate first the condition of that land, and then to enter upon the work of conversion for which I am taking chalices and all the necessary vestments of the Divine Cult. May it please Our Lord that the holy zeal of Your Majesty attain its end for the greater glory of the Divine One and the salvation of those souls.

May Our Lord keep the Catholic Royal Person of Your Majesty in His holy grace with health and complete felicity to the greatest good of Your vassals.

Your Majesty's humble servant and chaplain,

GABRIEL, Bishop of Cuba.

Havana,

August 14, 1674.

In the present material, the main narrative, addressed to the Queen of Spain, is written, as will be seen, in a clear hand, probably that of some secretary. It was accompanied by a brief note in the far less legible script of the Bishop himself, directed to the secretary of the

<sup>a</sup> Havana.

Council of the Indies. Dr. Wenhold has supplied the following translation of this epistle:

MY LORD:

In the despatch-ship which went out from here last month, I gave you felicitations on your elevation to the Secretaryship, then hoping to give them to you [also] as Secretary of State.

With this goes a packet to Her Majesty with my brief summary account of all that I have discovered in the territory of the provinces of Florida, conversions that I have made and characteristics of the Indians, [I] being by the Divine Mercy the first to tread those lands. And to the hands of the President went my map of the country. It is duplicated by this; and in the one [go] the original *autos* that have resulted from the visitation, and in the other an authenticated copy of them.

I remain at your service for all that you may be pleased to command me, to which I shall respond with good will. May God keep you many years.

Your humble servant kisses your hands,

GABRIEL, Bishop of Cuba.

Havana,

January 4, 1676,

To Señor Don Antonio de Rojas.

From the annotations accompanying this document it appears that it was "received with the galleons", taken up at the April session of the Council of the Indies, and referred to the attorney general, who stated that no report need be made in connection with it but that it should be kept in the office of the secretary. The Council took the action recommended on July 12, 1676, and it was furthermore commanded "that the Bishop be thanked for the work he has accomplished and urged to continue it."

From the same body of material Dr. Wenhold has obtained another letter from the Bishop, this one written in the same hand as the main document, presumably by that of the Bishop's secretary. It bears an earlier date than the above and was probably prepared immediately after Calderón returned to Cuba.

SEÑORA:

Your Majesty is pleased to command me, by the royal cédula of June 24, of this year, to apply some financial aid to the repairing of the convent of San Lorenzo el Real del Escorial.

The financial obligations, Señora, which I have, with the expenditures I made during the visit to the provinces of Florida, where I maintained eight months, at my own expense, a company of Spanish infantry of the Post [of St. Augustine], and two of Indians, arquebusiers and archers, because I had to traverse the frontier of the country of the Chiscas and Chichimecos, barbarous and warlike heathen, and with the construction of the main bastion of the wall of this city which I have done at my expense and that of the ecclesiastics, have made it impossible for me to do at this time what I shall do when my debts are paid.

May Our Lord keep the Catholic Royal Person of Your Majesty to the greatest blessing and comfort of your vassals.

Your Majesty's humble servant and chaplain,

GABRIEL, Bishop of Cuba.

Havana,

November 20, 1675.

The "Chiscas and Chichimecos" were probably two or more different bands of Yuchi. A matter of the very greatest interest to ethnologists and historians alike is the whereabouts of the maps mentioned in the text. As there were two copies, one of them at least should have survived.

Dr. Wenhold has supplied textual notes in connection with her translation of the Calderón narrative presented here, but I wish to add to these some references to important ethnological facts that it contains.

We have so little material regarding the old Florida tribes that any addition, however small, is most welcome, but in the present instance light is cast upon a number of specific problems of considerable importance.

It is interesting to know that the languages of "Guale, Timuqua and Apalache" were the three principal ones of the province but that is not unexpected. Much more important are the locations here given of the various missions, which will enable us to place the tribes approximately in their former seats. We also have the fact established that the Guacara Indians were originally on the Suwanee River. Another document, kindly referred to me by Dr. Wenhold and dating from early in the eighteenth century, shows that the present Wakulla River, which flows by St. Marks, was then known as the Guacara. This means that part, at least, of the Guacara Indians moved into the Apalachee country after 1675, or, possibly, at a still earlier date and that Wakulla is a corruption of Guacara since there was no *r* sound in the languages of the Apalachee, the Creeks, or any of their relatives.

In connection with the Bishop's treatment of the Apalachee province, we have supplied to us the exact dates of foundation of two of the missions and proof that some Apalachee towns consisted of recent invaders. The connection is established between the "Tama" Indians and the Yamasee. We have definite information that the Chines, Pacâras, and Amacânos were formerly independent units, and the separate enumeration of the last seems to show that the Yamacraw of Georgia history were distinct from the Yamasee.

Thanks to Bishop Calderón's connection with the Sawokli missions much is added to our knowledge of them, and we have the earliest known lists of the Lower and Upper Creek towns. We learn that in

1675 there was already an Oconee town on the Chattahoochee. This may have been an earlier position of the town later found on Oconee River or a separate settlement of the same tribe. We learn that Kolomi, which appears later as an Upper Creek town, was then among the Lower Creeks, and that the Hilibi were divided between the two sections of the nation. The Hitchiti and Okmulgee had seemingly moved over from Okmulgee River to be near the Spaniards. Three new towns appear among the Lower Creeks,—Chicahûti, Tacûsa, and Cuchiguâli—the first of which seems to contain the word huti, “home”, while the second resembles closely the name of the mole, “takusa”. A small Creek clan was so called.

Next we have information regarding the Chatot missions and a note on the Chiska or Yuchi. The list of Upper Creek towns, those given as constituents of the “Province of Toâssa”, is very incomplete. We recognize the Tawasa, Muklasa, Pacana, Hothliwahali (Oslibati), Okfuskee, Atasi, Tukabahchee, Hatcichaba, and Hilibi. Atayâche so closely resembles Atahachi, the name of the Mobile town visited by De Soto in 1540, that I am inclined to identify the two, all the more as Atayâche is enumerated along with the Alabama towns whose speech resembled that of the Mobile, though the locations of the two do not agree. I do not recognize Escatâna, Ilantalui, and Ichopôsi.

The notice of the Choctaw nation that appears here is the oldest under the name by which they are commonly known, and we learn that they were already very numerous.

In Cofâtache we seem to have a very late reference to Cofitachequi but unfortunately no clue to the affinities of the people so called except the fact that they controlled the Indians of Escamacu, who were apparently Muskogean.

Important is the localization near Pine Island of the place where De Soto had a small vessel built, since this was where Narvaez had previously constructed his own ill-fated crafts.

Students of early Indian population will be interested in the statement that in 1675 there were 13,152 Christianized Indians, for this must represent an actual enumeration.

To the controversy over Spanish mission buildings in the Southeast and the material of which they were made, our Bishop contributes the information that his Indians were “great carpenters as is evidenced in the construction of their wooden churches which are large and painstakingly wrought.”

Most of the words attributed to the Indians are either Spanish or—as instanced by *bujío* and *barbacoa*—from the Arawak language of



the West Indies, but *hurimela* is probably Timucua, in which language the word meaning "outside", or "in the forest", is *huri*. *Ojêo* may also be a Timucua word though I have been unable to translate it. *Athequi* is the Timucua form of the word which appears in Creek as *yatika*.

The description of the town house is peculiarly interesting since it shows that the northern Timucuan town houses, at least, were built like the town houses in the settlements of the Guale expatriates north of St. Augustine, as described by Dickenson. Perhaps the "very large cabin with a large open court in the middle" which De Soto's men found at Uriutina in central Florida was of this character. In any case, it would seem necessary to modify somewhat the size Calderón attributes to these houses when he says that they "can accommodate two to three thousand persons" but to increase the dimensions of their doorways.

The list of European trade objects will attract the attention of Florida archeologists.

*Supplementary notes supplied by Robert R. Otis, of Atlanta, Ga.*—The Queen to whom the Bishop addresses his letter was Queen Mariana, who was at the head of a Regency which governed Spain from 1665 to 1675, during the minority of Charles II. She was of the House of Austria, exceedingly religious, and much interested in the spread of Christianity in the New World, her policy being largely influenced by the Jesuit Father Nithard, who was also active in developing foreign mission fields. Calderón was appointed Bishop of Cuba in 1671, with headquarters at Santiago de Cuba, his jurisdiction embracing also the adjacent mainland sections of North America, known to the Spaniards as Florida. In 1673 the Queen Regent, acting in the name of the King, ordered a synod held in Florida by Bishop Calderón, and the following year he paid his visit to the mainland, not returning to Cuba until 1675. Writers having access to source materials show that he arrived in Florida August 23, 1674, while his last recorded act there was on June 21, 1675, which indicates that he spent 10 months in Florida lacking 2 days. The day after his arrival at St. Augustine he ordained seven young priests belonging to the best families, the first known instance in the territory of the present United States. On August 29 a formal reception was given him at the Franciscan Monastery at St. Augustine by Vicar General Perete. Father Englehardt, the California Mission historian (using source MSS.), says that during this year five missions were restored by him—Asao on St. Simons, one on Santa Catalina, one on Jekyll Island, San Jose on Sapello, and one at San Felipe, South Carolina. October 7, 1674, he issued orders forcing plantation owners to permit Indian workmen to attend divine service. For 8 months he traveled over this part of North America, enduring great hardships, and Englehardt says he spent \$11,000 to ameliorate the condition of both Indians and whites. He adds that it was probably in consequence of Bishop Calderón's demands upon the King that Father Moral was sent to Florida in 1676 with 24 Friars. Englehardt also says that Calderón died March 16, 1676, in consequence of hardships endured during his Florida visit.

## FLORIDA AND THE FLORIDA MISSIONS

SEÑORA:

What has been discovered, up to today, concerning the entire district of Florida, both along the seacoast and inland, is as follows:

On the coast of the northern border, 30 leagues from Cape Canaveral, [where] the canal of Bahama disembogues, is located, on the 30th parallel of latitude, the city of Saint Augustine which was founded about 1559<sup>1</sup> by the Adelantado Pedro Menendes Aviles. It is the capital of the provinces of Florida and has more than 300 Spanish inhabitants, soldiers and married people. Its harbor is very secure by reason of a very dangerous sand bar which it has at its entrance, which shifts its position in storms and at high tide has 20 spans<sup>2</sup> of water. The city is built lengthwise from north to south. It is almost cut off by an arm of the sea which surrounds it and buffets it, leaving it half submerged from hurricanes as it lies at sea level. Its climate is somewhat unhealthful, being very cold in winter, with freezes, and excessively hot in summer, both of which extremes are felt the more as there is no protection nor defence in the houses, they being of wood with board walls. The soil is sand and therefore unproductive; no wheat grows, and corn only sparsely and at the cost of much labor. Thus the inhabitants are compelled regularly to depend for their sustenance upon the products of the province of Apalache. The section does not produce any sort of raw material which could attract trade, and has no resources other than the government allowance which it awaits each year from the city of Mexico, and by which the infantry is fed and clothed.

As regards its spiritual welfare, it has a parish church dedicated to Saint Augustine, served by a priest, a sacristan and acolytes, and a Franciscan convent, headquarters for the province, called Saint Helena, with three monks, a superior, a preacher, a lay brother, and with authority by a royal decree of Your Majesty to have three curates for the three principal languages of these provinces, Guale, Timuqua and Apalache, for the teaching of Christian doctrine and the administering of the sacraments to the Indians who usually attend

<sup>1</sup> The city of Saint Augustine was actually founded in 1565.

<sup>2</sup> About 15 feet. One hundred years later the estimated depth of the water on the bar at low tide was 9 feet.

to the cultivating of the lands of the residents of the Post [Saint Augustine]. Of the four hermitages which formerly existed, only two remain: San Patricio and Our Lady of Solitude, and a hospital contiguous to the latter with six beds. For defense there is a fortress with 20 guns and a good garrison, a governor resident in the city, a sergeant-major, 2 captains, 300 enlisted men, and 2 royal officials.

Going out of the city, at half a league to the north there is a small village of scarcely more than 30 Indian inhabitants, called Nombre de Dios, the mission of which is served from the convent. Following the road from east to west, within an extent of 98 leagues there are 24 settlements and missions of Christian Indians, 11 belonging to the province of Timuqua and 13 to that of Apalache.

#### THE PROVINCE OF TIMUQUA

Ten leagues from the city of Saint Augustine, on the bank of the river Corrientes [the St. Johns], is the village and mission of San Diego de Salamototo. It [the river] is very turbulent and almost a league and a half in width. From there to the village and mission of Santa Fe there are some 20 uninhabited leagues. Santa Fe is the principal mission of this province. Off to the side toward the southern border, at a distance of 3 leagues, is the deserted mission and village of San Francisco. Twelve leagues from Santa Fe is the mission of Santa Catalina, with Ajohica 3 leagues away and Santa Cruz de Tarihica 2. Seven leagues away, on the bank of the large river Guacara, is the mission of San Juan of the same name. Ten [further on] is that of San Pedro de Potohiriba, 2, that of Santa Helena de Machaba, 4, that of San Matheo, 2, that of San Miguel de Asyle, last in this Timuquan, or Ustacanian, province.

#### THE PROVINCE OF APALACHE

Two leagues from the said village of Asyle is the mission of San Lorenzo de Hibitachuco, first village of this province. From this mission to that of La Concepción de Ayubali it is 1 league, and another to that of San Francisco de Oconi, another to that of San Juan de Aspalaga, 2 to that of San Joseph de Ocuya, 4 to that of San Pedro de Patali, 2 to that of San Antonio de Bacuqua, 2 to that of San Damian de Cupahica, called also Escambi, one to that of San Luis de Talimali which is the largest of all, another to that of La Purificación de Tama, called <sup>a</sup> Yamases, another to that of San Martín de

<sup>a</sup> This participle is plural, though why it is so is not clear.

Tomoli, 2 to that of Santa Cruz de Capoli, called also Chuntafu, and 4 from Tomoli to Assumpción del Puerto. Of these 13 missions 2, La Purificación de Tama and Assumpción del Puerto, both of which were heathen [villages], I founded on the 27th of January and the 2d of February of this present year 1675, gathering in Assumpción the three heathen nations, Chines, Pacâras and Amacânos, who are gradually being instructed and baptized. In the mission of San Luis, which is the principal one of the province, resides a military officer in a country house defended by pieces of ordnance and a garrison of infantry.

#### THE PROVINCE OF APALACHOCOLI

At 2 leagues from the afore-mentioned village of San Luís, on the northern frontier, is the river Agna which divides the provinces of Apalache and Apalachocoli, and at a distance of 12, on the bank of another large and copious river which takes its name from that<sup>4</sup> province and runs through it from north to south, is a heathen village called formerly Santa Cruz de Sabacola el Menor, now La Encarnación a la Santa Cruz de Sabacola, the church having been dedicated to this sovereign mystery on Thursday, February 28th of this year, wherein have gathered the Great Cacique of that province, with his vassals from Sabacola el Grande which I have converted to our holy faith, and which will be a large town and converted [area], especially as the 13 Apalachocolan villages which are on the bank of the river of that name, 30 leagues to the north, have offered to do likewise. These [villages] are: Chichahûti, Sabacôla, Ocôni, Apalachocôli, Ilapi, Tacûsa, Usachi, Ocmûlgui, Ahachito, Cazithto,<sup>5</sup> Colômme, Cabita, Cuchiguâli.<sup>6</sup>

Nine leagues from Encarnación, on the northern frontier, is another [village] named San Nicolás, of about 30 inhabitants, and 3 leagues further on is another, San Carlos, of something like 100 inhabitants. Both these are of the Chacatos nation, which 14 years ago requested baptism and had not their desire fulfilled until the 21st of June of last year, 1674. In that section, living in encampments without any permanent dwellings, are more than 4,000 heathen called Chiscas, who sustain themselves with game, nuts and roots of trees.

<sup>4</sup> *Aquella*, "the former", which should refer to the Apalache, but plainly the Apalachicola is meant.

<sup>5</sup> So spelled; usually known as Kasihita or Cusseta.

<sup>6</sup> Why the writer uses the circumflex on some Indian names and omits it from others is not at all evident.

Between the northeast and [north]west, about 30 leagues distant, on the bank of a large river, is the province of Toâssa, of barbarous heathen inhabitants, comprising 14 villages: Toâssa, Imocolâsa, Atayâche, Pacâni, Oslibâti, Afaschi, Escatâna, Atâssi, Tubâssi, Tiquipachi, Achichepa, Hilâpi, Ilantâlui, Ichopôsi.

Seventy leagues further on is the great and extensive province of the Chacta which includes 107 villages, and to one side, on the western frontier, on an island near the harbor of Spîritu Santo, is [the province] of Mobile, both these of barbarous heathen; this being all I have been able to discover, as in spite of having made diligent inquiries I have been unable to find anyone who could give me information concerning the territories of Penacho and Tanoyo which Marcos Lucio puts on his map supposing them to be in the neighborhood of the province of Apalachocoli. However, as he did not go further than the city of Saint Augustine, so distant from these provinces, and wrote only from vague hearsay, he may have erred in the names, and they may have been those of the afore-mentioned provinces of the Chacta and Mobile, for neither does he put on his map the villages of the provinces of Timuqua and Apalache, as Your Majesty will see from the chart I have made and send herewith.<sup>7</sup>

#### COAST OF THE NORTHERN FRONTIER

Out from Saint Augustine, along the seacoast toward the northern frontier, is the province of Guale, and in it are the following settlements:

At 2 leagues from the city is the village and mission of La Natividad de Nuestra Señora de Tolmato; at 10,<sup>8</sup> the village and mission of San Juan del Puerto at the bar of which disembogues the great river Corrientes, already mentioned; at 6, the mission and village of Santa María; at 3, San Phelipe; at 9, Santa Buanaventura de Guadalquini; at 6, Santo Domingo de Asahó; at 6, San Joseph de Zapala; at 2, Santa Catalina. All are settlements of Christian [Indians], and in the last named Your Majesty has an officer with a good garrison of infantry.

From there it is about 2 leagues to the bar of Asôpo, and from there one travels among shoals, bars and rivers<sup>9</sup> 14 leagues into the province of Escamacû, today subject to the Mico of Cofâtache, [where] near the village of Oristan is Saint Helena which was a village of Christians.

<sup>7</sup> Unfortunately not included with the photostatic copy of the document.

<sup>8</sup> All distances are measured from the last place mentioned unless otherwise specified, it seems.

<sup>9</sup> *dentro de bancos y fuera de barras y rios.*



and at 24 leagues [away] is Port Saint George, now an English settlement, distant 84 leagues from Saint Augustine. Fifteen leagues to the west, inland, is the province of Joâqui, where is the great lake in which, according to tradition, Fernando de Soto and his men saw many pearl oysters. From this province to that of Apalache, along the northern frontier, there dwells, in encampments, without fixed dwellings, the numerous nation of the Chichimecos, heathen, so savage and cruel that their only concern is to assault villages, Christian and heathen, taking lives and sparing neither age, sex nor estate, roasting and eating the victims.

#### COAST OF THE SOUTHERN FRONTIER

Traversing the coast along the southern frontier through the Bahama canal, passing the harbors of Matanzas and Mosquitos, 30 leagues from the city of Saint Augustine is Cape Cañaveral, whose shoals extend 6 leagues into the sea; and 8 leagues from it is the bar of Ais. At 5 is Guaxa, or Ropa Tendida; at 2, Jobe; at 7, Agea; at 4, Arroyo Seco from where one goes to Las Bocas and Cabeza de los Martyres, at which latter point disembogues a large river that flows into the large lagoon of Maymi where, according to tradition, there is, on a little islet in it, the treasure of a galleon which was lost on that coast. From this inlet one goes by sand banks and keys [inhabited by] savage Indians to the inlet called Carlos. From there to the bay of Espíritu Santo the direction coastwise is from northwest to southeast. Four leagues [beyond Carlos] is the bay of Tampa. At 6 from the Beach of Pusâle is the Pojoy river; at 12 is Tocopâcas.<sup>10</sup> It is 20 leagues to Majuro and 20 more to Guaza, 3 to the harbor of San Martín and 20 to that of San Marcos in the province of Apalache. From there one goes by an inlet of 18 leagues to Matacojo where, they say, Fernando de Soto built ships to navigate it. At 3 leagues from there the river Agna disembogues, and rounding the point of the cape which some call Apalache and others Hibineza, one comes to the inlet of Taxaquachile where the great river Apalachocoli empties.

On all this coast, from the afore-mentioned bar of Mosquitos, called Surruquê, to the river Tocopacâs, both on the islet which they call Cayos<sup>11</sup> and on the mainland, live 13 tribes of savage heathen Carib Indians, in camps, having no fixed abodes, living only on fish and roots

<sup>10</sup> "Is that of Tocopâcas", is what the writer actually says. "That", in Spanish, is here masculine, but so are "village" and "river", and the reference is therefore not very clear.

<sup>11</sup> The word *cayos* is in parentheses; why is not apparent.



of trees. These are: The Surruquêses, the Aÿses, the Santalûces, the Geigas, the Jobêses, the Vizcaynos,<sup>12</sup> the Matcumbêses, the Bayajondos, the Cuchiagâros, the Pojôyes, the Píneros, the Tocopâcas, and those of Carlos, who are great fishermen and divers.

#### CHARACTERISTICS OF THE CHRISTIANIZED INDIANS

In the four provinces of Guale, Timuqua, Apalache and Apalachicola there are 13,152 Christianized Indians to whom I administered the holy sacrament of confirmation. They are fleshy, and rarely is there a small one, but they are weak and phlegmatic as regards work, though clever and quick to learn any art they see done, and great carpenters as is evidenced in the construction of their wooden churches which are large and painstakingly wrought. The arms they employ are bow and arrows and a hatchet they call *macâna*. They go naked, with only the skin [of some animal] from the waist down, and, if anything more, a coat of serge without a lining, or a blanket. The women wear only a sort of tunic that wraps them from the neck to the feet, and which they make of the pearl-colored foliage of trees,<sup>13</sup> which they call *guano* and which costs them nothing except to gather it. Four thousand and eighty-one women, whom I found in the villages naked from the waist up and from the knees down, I caused to be clothed in this grass<sup>14</sup> like the others.

Their ordinary diet consists of porridge which they make of corn with ashes,<sup>15</sup> pumpkins, beans which they call *frijoles*, with game and fish from the rivers and lakes which the well-to-do ones can afford. Their only drink is water, and they do not touch wine or rum. Their greatest luxury is [a drink] which they make from a weed that grows on the seacoast, which they cook and drink hot and which they call *casina*. It becomes very bitter and is worse than beer, although it does not intoxicate them and is beneficial. They sleep on the ground, and in their houses only on a frame made of reed bars, which they call *barbacoa*, with a bear skin laid upon it and without any cover, the fire they build in the center of the house serving in place of a blanket. They call the house *bujío*. It is a hut made in round form, of straw, without a window and with a door a *vara*<sup>16</sup> high and half a *vara* wide.

<sup>12</sup> A Spanish word, like Santalûces, Bayajondos and Píneros.

<sup>13</sup> *Guano* is a general term for any sort of palm tree or leaf. He evidently refers to clothing of Spanish moss.

<sup>14</sup> *Yerba*: the use of this word indicates that the writer did not recognize the material.

<sup>15</sup> Corn with ashes" = lye hominy.

<sup>16</sup> The *vara* is 2.8 feet.

On one side is a granary supported by 12 beams, which they call a *garita*, where they store the wheat, corn and other things they harvest.

During January they burn the grass and weeds from the fields preparatory to cultivation, surrounding them all at one time with fire so that the deer, wild ducks and rabbits, fleeing from it fall into their hands. This sort of hunting they call *hurimelas*. Then they enter the forests in pursuit of bears, bison and lions which they kill with bows and arrows, and this they call *ojêo*. Whatever they secure in either way they bring to the principal cacique, in order that he shall divide it, he keeping the skins which fall to his share. Offering is made to the church of the best parts, and this serves for the support of the missionary priest, to whom they are in such subjection that they obey his orders without question.

In April they commence to sow, and as the man goes along opening the trench, the woman follows sowing. All in common cultivate and sow the lands of the caciques. As alms for the missionaries and the needy widows, they sow wheat in October and harvest it in June. This is a crop of excellent quality in the province of Apalache, and so abundant that it produces seventy *fanegas*<sup>17</sup> from one *fanega* sown.

Each village has a council house called the great *bujio*, constructed of wood and covered with straw, round, and with a very large opening in the top. Most of them can accommodate from 2,000 to 3,000 persons. They are furnished all around the interior with niches called *barbacôas*, which serve as beds and as seats for the caciques and chiefs, and as lodgings for soldiers and transients. Dances and festivals are held in them around a great fire in the center. The missionary priest attends these festivities in order to prevent indecent and lewd conduct, and they last until the bell strikes the hour of *las ánimas*.

These Indians do not covet riches, nor do they esteem silver or gold, coins of which do not circulate among them, and their only barter is the exchange of one commodity for another, which exchange they call *rescate*.<sup>18</sup> The most common articles of trade are knives, scissors, axes, hoes, hatchets, large bronze rattles,<sup>19</sup> glass beads, blankets which they call *congás*, pieces of rough cloth,<sup>20</sup> garments and other trifles.

<sup>17</sup> A *fanega* is about a bushel and a half.

<sup>18</sup> *Rescate* is a good Spanish word of Latin origin, meaning "ransom" but with "barter" as a secondary meaning.

<sup>19</sup> *Cascabeles grandes de bronce*. *Cascabeles* are properly small bells of the type used on harness.

<sup>20</sup> *Jerguetas*.

As to their religion, they are not idolaters, and they embrace with devotion the mysteries of our holy faith. They attend mass with regularity at 11 o'clock on the holy days they observe, namely, Sunday, and the festivals of Christmas, the Circumcision, Epiphany, the Purification of Our Lady, and the days of Saint Peter, Saint Paul and All Saints Day, and before entering the church each one brings to the house of the priest as a contribution a log of wood. They do not talk in the church, and the women are separated from the men; the former on the side of the Epistle, the latter on the side of the Evangel. They are very devoted to the Virgin, and on Saturdays they attend when her mass is sung. On Sundays they attend the *Rosario* and the *Salve* in the afternoon. They celebrate with rejoicing and devotion the Birth of Our Lord, all attending the midnight mass with offerings of loaves, eggs<sup>21</sup> and other food. They subject themselves to extraordinary penances during Holy Week, and during the 24 hours of Holy Thursday and Friday, while our Lord is in the Urn of the Monument,<sup>22</sup> they attend standing, praying the rosary in complete silence, 24 men and 24 women and the same number of children of both sexes, with hourly changes. The children, both male and female, go to the church on work days, to a religious school where they are taught by a teacher whom they call the *Athequi*<sup>23</sup> of the church; [a person] whom the priests have for this service; as they have also a person deputized<sup>24</sup> to report to them concerning all parishioners who live in evil.

Your Majesty's most humble servant and chaplain,

GAB'L<sup>25</sup> Bishop of Cuba.

<sup>21</sup> Spelled *guebos*.

<sup>22</sup> *En la Urna del Monumento*.

<sup>23</sup> *Athequi*; Indian word meaning "interpreter".

<sup>24</sup> The word here translated "person deputized" is *fiscal*, which means "attorney" or "prosecutor", but neither of those terms seems to the translator to fit the case.

<sup>25</sup> *Gabriel*; abbreviated thus.

Señora

Lo que oy está descubierto en todo el  
distrito de la Florida así por la costa  
de la mar como por la parte de tierra  
es lo siguiente  
En la costa de la vanda del norte a pinto a  
leguas del caue de canaveral desembocada  
la canal de Bahama esta en treinta gra-  
dos de altura la Ciudad de S. Agustín que fun-  
do por los años de mil quinientos y cinquien-  
ta y nueve el Adelantado Pedro Meléndez,  
Aguila, Cauza de las Prouincias de la fidei-  
da que tiene mas de trescientos vecinos espa-  
ñoles soldados y casados; su Puerto es muy se-  
guro por una barra de arena muy peligrosa  
que tiene ala entrada de el que se muda con  
las temporales y en plena mar nase veinte  
y palmas de agua. La Ciudad tiene su asien-  
to por lo largo de norte a sur, esta casi i-  
slandada de un trazo de mar que la circun-  
da y maltrata, dexandola mucho anegada  
con los huracanes por estar en un llano igual  
con el agua. Su temple es poco saludable  
padeciendo en Hibierno grandes frios y cla-  
uides; y en verano excecivos calores, que tanto  
mas lo uno y otro es sensible quanto mas  
figaro alguno ni defensa en las casas por  
ser de madera y las paredes de tablas, el  
terreno es de arena y por esto muy estéril  
de frutos donde no da el trigo, y el maíz  
muy escaso y acosta de mucho sudor, necesi-  
tando de ordinario de valere los vecinos  
para su sustento de la Prouincia de

Apalache. La tierra no produce yeros de mer-  
caderia que incite la codicia de los comercios  
y solo tiene por aliado el situado que cada  
año espura de la Ciudad de Mexico con que  
se sustentan y vive la Infanteria.  
Para lo espiritual tiene una Iglesia Parro-  
quial dedicada a S. Aug. que sirven un  
Cura Sacristan y moracillos. E un convento  
de la Religión de S. fran. Cauza de la Cruz  
llamada S. Helena con tres Religiosos, Guar-  
dian, Predicador y un lego, y facultad por  
Real Cedula de N. M. para tener tres muni-  
dos doctores de las tres lenguas mas co-  
munes de estas Provincias, que son Guale  
Timuqua y Apalache, para la ensenanza  
de la Doctrina Christiana y administracion  
de los Sacramentos a los Indios que de ordi-  
nario asisten en aquel Puesto a la labor  
de las tierras de los vecinos. De quatro flor-  
mitas que havia, solo han quedado dos  
S. Patricio y Nra S. de la Toledad y un ho-  
pital contiguo a esta con sus camas. Egara  
la defension una fortaleza con veinte plazas  
e buena guarnicion. un Gobernador que asi-  
ste en la Ciudad, Sargento mayor, dos ca-  
pitanes, trescientas plazas y dos oficiales  
Reales.  
E saliendo de la Ciudad a media legua ha-  
cia el norte ay una pequena Aldea depoc-  
mas de treinta Vecinos Indios llamada el  
nombre de Dios cuya Doctrina se sirve de  
de el convento. E siguiendo el camino  
Este a buelte en distancia de noventa y  
ocho leguas estan veinte y quatro Paro-  
quias y Doctrinas de Indios Christianos  
que de la Provincia de Timuqua y Guale  
de la de Apalache.



### Provincia de Timuqua

A diez leguas de la Ciudad de S. Aug. en la  
 Nueva del gran Rio de Comientes esta el  
 Lugar y doctrina de S. Diego de Salomote,  
 es muy tormentoso y casi de legua y media  
 de ancho. desde el, se va por despo. blado de  
 Punt. Aguas al Lugar y doctrina de S.  
 fee que es la principal desta Punt. y aun  
 tado a la Vuelta del sur en distancia de  
 tres leguas la Doctrina y lugar de San  
 Juan. que esta despo. blado, y desde S. fee  
 a doce leguas la de S. Est. y a tres la de  
 Abotica. y a dos la de S. Cruz qe. Pari  
 tica. y a siete a la Vuelta del gran  
 Rio de Guacara la de San Juan del  
 nombre. y a diez la de S. Pedro de Poto  
 biriba. a dos la de Santa Victoria de  
 Alacabala. a quatro la de S. Matheo. y a  
 dos la de S. Miguel de Ayole Vuelta de  
 esta Provincia Timuquara o Vtacana.

### Provincia de Apalache

Desde el Lugar de Ayole referido a dos  
 leguas esta la Doctrina de S. Tor. de Vi  
 ctachuco primer lugar desta Punt. de esta  
 Doctrina ala de la Concep. de Ayubali  
 y una legua y otra ala de S. Fran.  
 de Ocoru. y otra ala de S. Juan de Ho  
 palaza. dos ala de S. Joseph de Ocuya  
 quatro ala de S. Pedro de Patali. dos ala  
 de S. Antonio de Bacuqua. dos ala de  
 S. Damian de Cupabica por otro nombre  
 esambi. una ala de S. Luis de Tali  
 mali que es la mayor de todas. otra a  
 la de la Pariguan. de la Santa Hanna  
 dos Pimara. otra ala de S. Martin del



Somoli. dos ala de S.<sup>a</sup> Cruz de Capoli por otro nombre Chintafu. y desde la de Somoli quatro ala de la Assump.<sup>o</sup> del Puerto. Destas tres Doctrinas las dos que son la de la Purificacion de la Puma y Aniquion del Puerto que ambas eran de gentiles, se fundaron aora nuevamente en veinte y siete de febrero y dos de febrero del presente año de setenta y cinco congregadas en esta ultima de la Assumpcion las tres naciones de Gentiles, Chines, Pacáras, y Amacáron, que se van Catolicizando y baptizando. En la Doctrina de S. Luis que es la principal de la Provincia reside un tit.<sup>o</sup> de Gobernador en una Casa de campo con la defenza de diez y seis de artilleria y guarnicion de Infanteria.

### Prov. de Apalachicola.

Atos segun del lugar de S. Luis referido esta por la vanda del Norte el Rio del Agila que divide las Provincias de Apalache y Apalachicola. y en distancia de doze ala nueva de otro grande y caudaloso que toma el nombre de aquella Provincia y corre por ella de norte a sur, en lugar de gentiles llamado antes S.<sup>a</sup> Cruz del Sabacola el menor, y la Encarnacion ala S.<sup>a</sup> Cruz de Sabacola por haver dedicado la Iglesia a este tan soberano misterio el jueves veinte y ocho de febrero del presente año donde se agrega el Cacique mayor de aquella Prov. con sus Varatos de Sabacola el grande que se reducidos a una S.<sup>a</sup> fe y son una gran poblacion e conversion mayor<sup>te</sup> quando han ofrecido

hacer lo mismo los trece lugares Apalachocolis que estan alla fuera del mismo Rio en distancia de treinta leguas hacia el Norte; y son Chichabiki. Sabacola. Ocóni. Apalachocoli. Elapi. Jacura. Vacki. Ocmulqui. Alsa. Chito. Cazitito. Colomine. Cabita. Cucbi-guáli.

A nueve leguas de el de la Encarnacion alla Vanda del Norte otro nombrado S. Nicolas de poco mas de treinta Vecinos y tres adelante otro de S. Carlos de poco mas de ciento; ambos de la nacion de los Chacatos que ha via catorce años pedian el baptismo y nose les cumplio su deseo hasta el dia veinte y vno de Junio del año pasado de seiff cientos y setenta y quatro. En aquel parage en Vencherias sin poblaciones fixas, estan avicinados mas de quatro mil gentiles llamados Chiscas que se sustentan de la caza nueces y rayces de arboles.

Entre el Norueste y Nueste appco mas de treinta leguas de distancia alla fuera de un Caudaloso Rio, esta la Prov. de las Joana de barbaros gentiles que comprehen de catorce lugares. e son Joana. Emocola. Atayache. Pacari. Oslibati. Afaschi. Escatana. Aian. Subani. Aquipachi. Achi. Chaga. Hilipi. Elantalui. Chagóni.

A sesenta leguas adelante la grande y dilatada Prov. de la Chacta que comprehende ciento y siete lugares y aun Vado a la Vanda del Oriente en una isla cerca del grande Puerto del Spitu S. La de la Aboba ambas de Barbaros Gentiles que es todo lo que he podido descubrir sin hallar persona que me diese noticia (por Gracia diligencias que hice) de los Reynos

del Pinacho y Parígo que pone Marco Lu  
 En su Mapa suponiendo están vecinos a la  
 P. de Apalachicola, sino es que como no  
 paso de la Ciudad de S. Aug. tan distante  
 de aquellas P. de N. lo escribo por noticia  
 vagar fírrase los nombres q fueren las P.  
 runcias de la Chata y Mobila referidas, p  
 es tan poco pone en su Mapa los Pueblos de  
 las Plouindas de Simiqua y Apalache  
 que vera V. M. por la planta que he he  
 cho y venito con esta -

### Costa de la Yanda del Norte

Saliedo de la Ciudad de S. Aug. alia costa  
 de la mar de la Yanda del Norte, esta la Pro  
 uincia de Guale y en ella las Poblaciones  
 siguientes.

Ados leguas de la Ciudad el Lugar y Doctrina  
 de la Natividad de Nra Sra de  
 Holomato. y a diez el Lugar y doctrina de  
 San Juan del Puerto por cuya boca desuen  
 boca el gran Rio de Corrientes referido.  
 a seis la doctrina y Lugar de S. Maria  
 a tres la de S. Felipe. a nueve la de  
 S. Buena ventura de Gualquiri. a seis  
 la de S. Domingo de Asabó. a seis la  
 de S. Joseph de Zapala. y ados la de S.  
 Cap. que todas son Poblaciones de Ngras  
 nos y en esta Y. tiene V. M. un Cabo con  
 buena guarnición de Infanteria

De alli se va dos leguas ala barra de Asó  
 po y de ella por dentro de bancos y fueras  
 de barras y rios en catorce leguas de distan  
 cia en la P. de Cocamán sujeta oy al  
 Mico de Cofitache, cerca del Lugar del  
 Oristari. esta el de S. Helena que fue de  
 Christianos. y a veinte y quatro leguas el  
 Puerto de S. Jorge, oy población de Ngras

distante ochenta y quatro de S. Aug. y la tierra  
adentro hacia el poniente a quince leguas  
la Pcion. de Tiaqui, donde esta la gran la-  
guna en que es tradicion Neron Fernando  
de Soto y su gente muchas cosas de perlell.  
Desde esta Pcion. hasta la de Apalache por  
la vanda del norte habitan en Tamenacha  
sin poblaciones la nacion de los Chichimecos  
muy numerosa. Gentiles tan barbaros y crue-  
les que todo su fin es saltar los zaguas  
asi de Christianos como de Gentiles qui-  
tandoles las vidas, sin perdonar qual se-  
xo, ni estase asuandolos y comiendolos.

### Costa de la Vanda del Sur.

Corriendo la costa ala Vanda del Sur  
por la canal de Bahama pasando por los  
Puntos de Matanzas y Morquitos a trein-  
ta leguas de la Ciudad de San Aug. esta  
el Cauo de Canaveral, cuyos bajos salen  
seis leguas ala mar, y de el en distancia  
de ocho leguas esta la barra de Mr. y  
a cinco esta Guaxa o Topa tendida. ados  
Tobe. Sete Agea. quatro arroyo seco del  
a donde vera alas bocas y Causa de lo Mar  
torres, y por la Vltima desemboca en Rio  
grande que entra en la gran laguna del  
Maym, donde es tradicion ay en una  
Isla de ella un tesoro de N. Falcon que  
se pedio en aquella costa. desde esta boca  
se va por glaciets y Cayos de Indios barba-  
ros hasta la ensenada llamada de Car-  
los: y de ella ala Vija del Spiritu san-  
to es costa de Norueste a Sueste, y a  
quatro leguas esta el Puerto de Tampa. y  
la seis ala playa de Pusale el Rio del Po-  
toy, ados el de los Socopicas. veinte al



Maizuro, y otras Puente a Puente, y tras el Puerto de S. Martín y a Puente el de S. Marcos. Puente de Apalache y desde el sera por una enserada de diez y ocho leguas a Matucoso donde dicen fabrico Fernando de Soto vizcaínes para navegarla, y otras leguas de ella desemboca el Rio del Agria, y doblando la punta del Cauo que llaman de Apalache y otros de Jilimiza sera ala enserada del Guayachile donde desemboca el gran Rio de Apalachocoli.

En toda esta costa desde la barra de Morquitos referida que llaman de Sarruquie hasta el Rio de los Cocopacas asi en Sileru que llaman (cayos) como en tierra firme habitan once naciones de Indios Dieriles Caribes en Rancherías sin tener lugar fijo, sustentandose solo de pescado y Cayas de arboles que son Sarruquies. Ayres. Santalices. Delgas. Tobies. Vizcaynos. Matacumbies. Baya. Seridos. Cuchigágaros. Cofeyes. Piricos. Focopacas, y los de Carlos que son grande pescadores y buzos.

#### Proximidad de los Indios Aghanos.

En las quatro Ptos. de Guale Sirluaga Apalache y Apalachocoli ay trece mil Ciento y Cinquenta y dos Indios Aghanos, quienes administran el S. Sacram. de la Confirmación son Copulentes, y raro se halla pequeño, mas débiles y flacuos para el trabajo, aunque ingeniosos y presto de aprender qualquier arte que ven obrar, y grandes Curanderos como se ve como en las fabricas de las Iglesias de madera, grande industria en la labradura. Las armas de que usan son arco, flechas, y una machueta q. llaman Macana.

Andan en Carnes con sola vna piel de la cintura  
 abaxo, y el que mas vna casaca de Serquilla  
 sin ayorro, y vna frazada. & las mugeres con  
 sola vna como basquiria que les coge desde  
 el cuello hasta los pies que hazen de ver-  
 ba de los arboles de color de perla que  
 llaman Guano, y no les queda mas de coger  
 lo. La quatro mil y ochenta y vna que na-  
 tie en los Pueblos de la P. de Apuluche  
 desnudas de la cintura arriba, y de la ro-  
 dilla abaxo haze vestir desta Perba co-  
 mo las demas.

Su sustento ordinario es mas gachas q hazen  
 de maiz con Zenina, Calabazas, Judias que  
 llaman Frijoles y la Caza, y pesca de Rio  
 y lagunas que pueden alcanzar los mas bien  
 acomodados. La bebida es el agua sin  
 gustar el vino ni aguardiente, y el mayor  
 regalo es la que hazen de vna Perba que ay  
 en la costa del mar que cuagen y beben  
 caliente, & llaman Cagira, q. amarga mu-  
 cho, & es peor que la Cerbeja aunq. no le  
 emeraga, & haze prouecho. Quieren en el  
 suelo, y en sus casas solo sobre vn armador  
 de varillas de cana, que llaman barbaira  
 con vna piel de oso encina sin otro abri-  
 go, sustentados de mantala Lumine que  
 hazen en medio de la casa, que llaman  
 bufo, y es vna Chiza de paxa en forma de  
 donaa sin ventaria y la querta de ma  
 ra de alto, y media de ancho, y a un lado  
 haia vna sustentada de azucaras que  
 llaman garita donde recogen el trigo, ma-  
 iz, y lo demas de sus cosechas.

Por bien quemar la Perba y maliza de los  
 campos para labrarlos cercan de los aun tiem-  
 po de fuego, con que los Vinados, Caro &



Alrededor, y conexas, huyendo de él, dan en sus  
manos, y así se llaman las *burimelaf*.  
Acuada entran por la espesura de los mator-  
rales de los árboles, Cebollas y Leones que  
matan a flecheros, y la llaman *ofeo*, y to-  
do lo que en una obra cogen traen al cargo  
que Principal para que lo reparta, el qual  
se queda con las pieles que se tocan y de lo  
mas ofrenda a la Iglesia que sirve para  
el Religioso doctrinero a quien viven con tanta  
sujecion que sin replicar obedecen sus  
órdenes.

Por abril comienzan a sembrar y como va ca-  
rriendo el Varon le sigue la muger sembran-  
do, y todos en comun labran y siembran las  
siembras a los Caziques y de Limosna a los Re-  
ligiosos Doctrineros y Viudas necesitadas. El  
Trigo siembran por octubre y siegan por  
junio. Este se coge y de buena calidad  
en la Prov. de Apalache y con tanta abun-  
dancia que da setenta fanegas por una de  
siembra.

Todos los lugares tienen casa concilio que  
llaman el *busio* grande, que es de madera  
cubierto de gaxa en forma redonda, con  
una claraboya muy grande en lo alto, y los  
mas, capaces de dos y tres mil personas, ados-  
nados en contorno por la parte interior del  
nichos que llaman *barbacoas* y sirven de  
camas y asientos a los Caziques y Principa-  
les y de alojamiento a los soldados y  
pasajeros. Heran en ellos los bayles y fe-  
tes en contorno de una gran hoguera  
que hacen en medio de ella, a los quales asiste  
el Religioso doctrinero por sujetar lo inde-  
cente y deshonesto y duran hasta que se tu-  
ca a las animas.

No codician riquezas ni estiman las hon-  
ras.

Ni ora, cuya moneda no corre entre ellos, y solo cambian un genero por otro que llaman cate; y lo que mas corre es, cuchillos, tijeras, machas, azadas, hachuelas, cascabeles grandes de bronce, quantas de abalorio, maritales que llaman congas, oxequetas, paños y otras menudencias.

Quanto a la Religión no son Idolatras, y acuden con deuoción los misterios de nra. S. fe acuden con puntualidad a Misra alas once los dias festiuios que guardan que son los Domingos del año, y los dias de Natiuidad Circumcisión, Epiphania, Purificación de Nra. S. S. Pedro y S. Pablo, y el de todo S. y antes de entrar en la Iglea trae cada uno de offrenda ala Casa de Religión un haz de Leña, no hablan en la Iglea y estan divididos las mugeres al lado de la Epistola y los hombres al lado del Euañ. Son muy deuotos de Nra. S. y assi asisten los abalorios a la Misra cantada y los Domingos por la tarde al Rosario y saluen. Celebran con toda festiuidad y deuoción el Nacimiento de Nro Señor acudiendo todos a la Misra del Salto, con offrenda de bollos guisos, y otras cosas comestibles. Hazen penitencias extraordinarias en la semana Santa, y en las veinte y quatro horas del Jueves y Viernes S. que es la Nra. S. en la Vena del Monumento asisten en pie rezando con todo silencio el Rosario veinte y quatro hombres y veinte y quatro mugeres y otros tantos paxiculos de ambos sexos mudandose por horas. Los niños assi varones como hembras acuden los dias de trauaño por la mañana alas Igleas ala Doctrina Christiana que les ensena Nra.

Maestro de ellos, y llaman Abtegui de Na  
Iglesia, que tienen los Religiosos para es Fe  
ministerio, y m fiscal para que les de quen  
ta de todos los feligreses q. viven mal.

Enna

Los Sumos de inado y Caga de W

Enna de la que se abusa en  
los monasterios y conventos  
debe y se debe conser-

José de Caba

Enna de la  
de la de la  
de la de la

SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 17

# A NEW RACE OF THE SONG SPARROW FROM THE APPALACHIAN REGION

BY

ALEXANDER WETMORE

Assistant Secretary, Smithsonian Institution

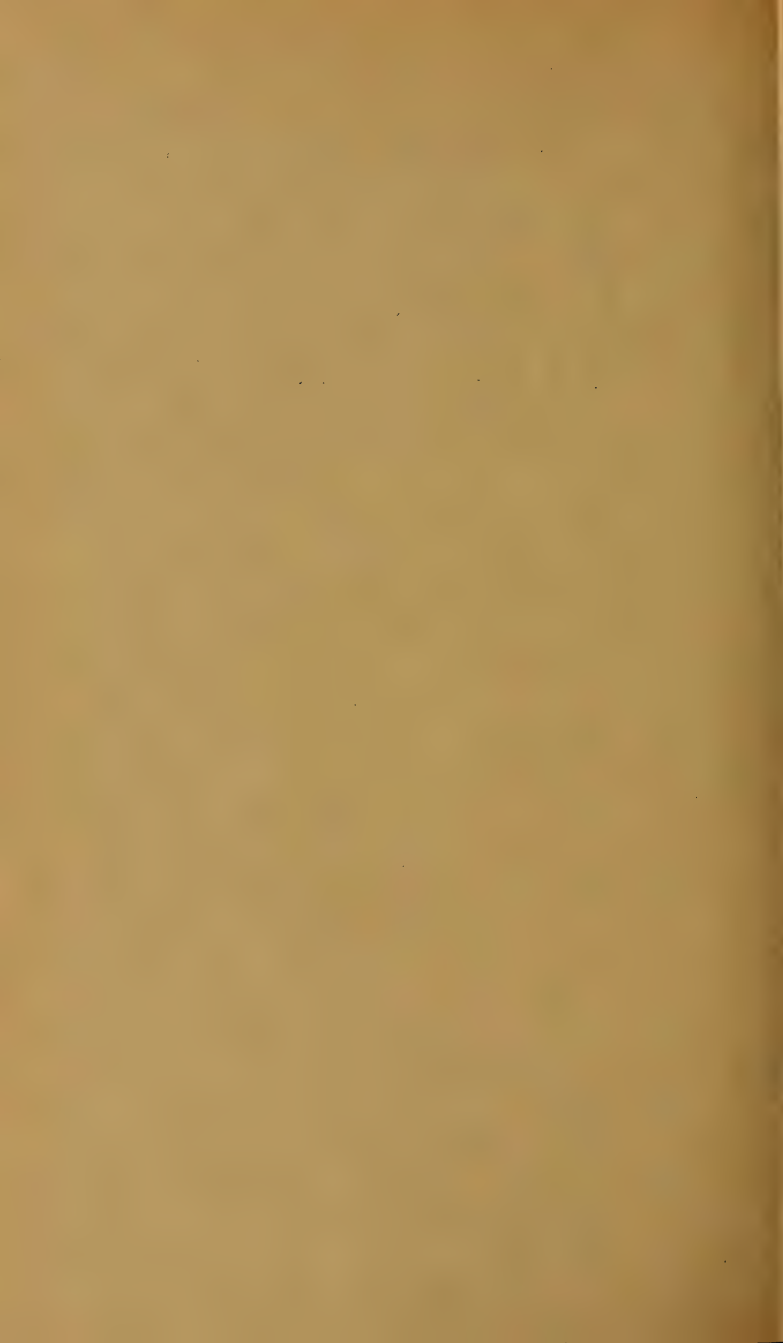


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## A NEW RACE OF THE SONG SPARROW FROM THE APPALACHIAN REGION

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*Assistant Secretary, Smithsonian Institution*

For some time the United States National Museum has been accumulating song sparrows to determine the distribution of the races of this bird in the middle section of the eastern United States, with results of considerable interest. In collections made during the past field season by a party financed by the Smithsonian Institution important specimens were obtained in West Virginia that indicate a hitherto unrecognized race. The new form may be known as

### MELOSPIZA MELODIA EUPHONIA, n. subsp.

*Characters.*—Similar to *Melospiza melodia melodia* (Wilson) <sup>1</sup> but distinctly darker above, being grayer, with the dark markings generally more distinct; sides of head grayer, less buffy or brown; tail averaging darker.

*Description.*—Type, U.S.N.M. no. 348887, ♂ adult, collected in the Cranberry Glades, Pocahontas County, W. Va., at an elevation of 3,300 feet, June 8, 1936, by W. M. Perrygo and C. Lingeback, original no. 393, in somewhat worn breeding dress. Sides of crown chestnut-brown, with the centers of the feathers dull black, and an indistinct line of light grayish olive down the center; superciliary stripe white washed with pale olive-gray; ear-coverts smoke-gray with a slightly buffy tinge, streak behind eye and another below ear-coverts between auburn and chestnut-brown; feathers of back dull russet with heavy black spots at tips, and an indistinct edging of pale olive-gray; rump feathers and upper tail coverts snuff-brown with indistinct blackish spots at tips; tail (considerably worn) fuscous black, edged with snuff-brown, the edging broad at base; lesser and middle wing-coverts dull russet; greater wing-coverts cinnamon-brown on exposed portions, blackish centrally; median and greater coverts with indistinct edgings of pale olive-gray; exposed surface of tertials black, edged with cinnamon-brown; primaries and secondaries fuscous black, the secondaries edged with cinnamon-brown, and the primaries mar-

<sup>1</sup> *Fringilla melodia* Wilson, Amer. Orn., vol. 2, 1810, p. 125, pl. 16, fig. 4.

gined indistinctly with light olive-gray; below white with the throat immaculate; a streak on either side of the throat dull black with an edging above of russet; feathers in center of breast with heavy black apical spots bordered with russet, forming a distinct dark central spot; on either side smaller triangular points of black, bordered more or less with russet, becoming longer, mixed with more brown, on sides and flanks; under tail coverts with centers bister margined with snuff-brown; tibiae cinnamon-brown.

*Measurements* (of type).—Wing 66.4, tail 66.6, culmen from base 13.2, tarsus 21.6 mm.

*Remarks*.—For a number of years I have been examining eastern song sparrows with much interest, and for some time it has been evident that the breeding birds of the Alleghany Mountain region constituted a darker race than typical *melodia*. For a time I have followed Todd<sup>2</sup> in calling this darker race *Melospiza melodia beata* Bangs,<sup>3</sup> a name that Todd has applied to the song sparrows of the region west of and including the Appalachian Mountains.

Recently through the assistance of Dr. Thomas Barbour and James L. Peters, of the Museum of Comparative Zoölogy, it has been my privilege to examine the type of *beata* to find that it is not the so-called Mississippi song sparrow but is similar to the birds of the northern plains region. It is identified as *Melospiza m. juddi* Bishop, of which *beata* becomes a synonym. The type agrees with *juddi* in the distinctly light gray cast of the upper surface, with prominent dark markings, though it is slightly darker than a series of that race from the typical area in North Dakota. As one goes farther north, into Canada, specimens that must be called *juddi* become slightly darker, and also among these is often found the large, heavy bill that Bangs noted in describing his type.

It will be recalled that *beata* was based originally on two specimens in the Bryant collection taken at Enterprise, Fla., on April 17, 1859. The southeastward line of migration for many birds of central Canada is now well established, so that the presence of a bird from this area in Florida is not to be considered unusual. The late date also fits in this same picture, for though song sparrows may be nesting in the central United States in April, the breeding grounds of individuals migrant from the northern part of the range of *juddi* may still be closed by winter conditions, so that such birds may linger in the south.

<sup>2</sup> Auk, 1930, p. 257.

<sup>3</sup> *Melospiza melodia beata* Bangs, Proc. New England Zool. Club, vol. 6, June 5, 1912, p. 87 (Enterprise, Fla.).

This identification incidentally adds another bird to the list of those known from Florida.

The bird of the mountain area selected as the type locality of *M. m. euphonia* is distinctly darker than specimens from the lowland regions of Tennessee, Kentucky, Indiana, and Illinois. As birds from this area are close to *euphonia*, for the present I identify them as of that race, though it appears that with more material they may be distinguished as distinct. The name *euphonia* will therefore for the present at least replace *beata* as given in the fourth edition of the A. O. U. Check-list of North American Birds (page 357).

The typical series of *euphonia* includes, in addition to a number of skins from the Cranberry Glades, specimens from Cheat Mountain above Cheat Bridge, and Middle Mountain 12 miles northeast of Durbin, in West Virginia. Breeding birds from White Pine, Rocksdale, Philippi, Big Bend, Zela, Drennen, and Muddlety, W. Va., are intermediate toward the lighter, lowland group. The mountain bird extends into Virginia at Pulaski and is the form of White Top Mountain, where with Dr. J. J. Murray I found it in Elk Garden at an elevation of 4,400 feet at the head of Big Helton Creek. Specimens secured by Dr. Murray and me near Sturgills, Jefferson, and Warrentonville, N. C., and Independence, Va., are also this form. Birds from Shawsville and Christiansburg, Va., are intermediate toward *melodia*, as is one from Lexington, Va., and another from Lost River near McCauley, W. Va., but are best identified from the few skins at hand as *euphonia*. A skin from Halltown, W. Va., seems to represent true *melodia*.

To the north I find that breeding specimens from Sayre and Silver Lake, Pa., and Canandaigua Lake, N. Y., are also to be identified as the race *euphonia*.

It may be noted that in common with other races of the song sparrow in the East, *euphonia* shows a distinctly rufescent phase in many individuals. A breeding bird that I collected personally at the type locality in the Cranberry Glades has the brown markings (auburn in color) predominating over any other shade on the dorsal surface.

It has seemed appropriate to me to name this new race *euphonia* from the cheerful song common to all races of the song sparrow throughout its extensive range.



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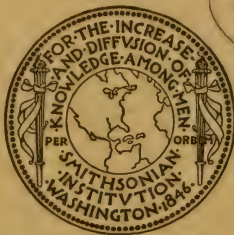
TWO ORIGINAL PHOTOGRAPHIC NEGATIVES  
OF ABRAHAM LINCOLN

(WITH FOUR PLATES)

BY

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## TWO ORIGINAL PHOTOGRAPHIC NEGATIVES OF ABRAHAM LINCOLN

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*Assistant Secretary, Smithsonian Institution*

(WITH FOUR PLATES)

Among recent accessions in the Section of Photography of the United States National Museum there are two original photographic negatives of Abraham Lincoln that are of great interest as they present an outstanding figure in American history at an important point in his career. These negatives have come to the national collections through the Post Office Department.

According to the records accompanying them, the two negatives in question were made by Alex. Hesler of the Hesler Studios, located in early years at 113 Lake Street, Chicago, Ill. Sometime after the presidential election of November 1860, and before the inauguration of the following March, friends of Mr. Lincoln arranged to have Hesler go to Springfield, Ill., where the President-elect sat for the photographer. The usual wet plate process of the period was used, with results that are reported to have been satisfactory and pleasing both to Lincoln and to his friends.

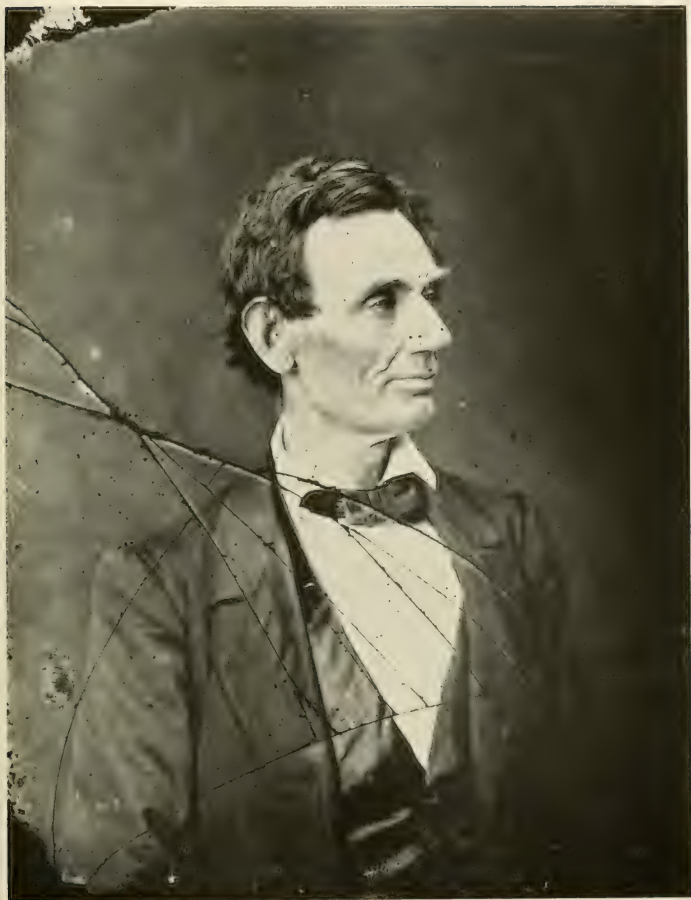
When Hesler retired from business, his studio came into the possession of George B. Ayres, who removed later to Buffalo, N. Y., and then to Philadelphia, Pa., taking these negatives with him—a fortunate circumstance, as otherwise they probably would have been destroyed in the Chicago fire of 1871. Mr. Ayres' property in time passed to two daughters, Mrs. Edith L. Bunce and Anne Smith Ayres, the latter coming into sole possession of the Lincoln negatives on the death of Mrs. Bunce. After Miss Ayres' death they were purchased from her estate by William H. Woodward, of Philadelphia. During shipment by parcel post to St. Louis in 1933 the negatives were accidentally broken, which led to their acquisition by the Post Office Department in settlement of a claim for damage.

In the course of this settlement the postal authorities made an extended investigation, which through the advice of experts established without question the authenticity of the photographic plates as originals. Realizing their great historical importance, the Post Office

Department transferred the negatives, through W. W. Howes, First Assistant Postmaster General, in a letter dated January 22, 1935, to the United States National Museum for permanent preservation as part of the national collections. They were placed directly in the hands of the writer by the Superintendent of the Division of Dead Letters and Dead Parcel Post on January 29, 1936.

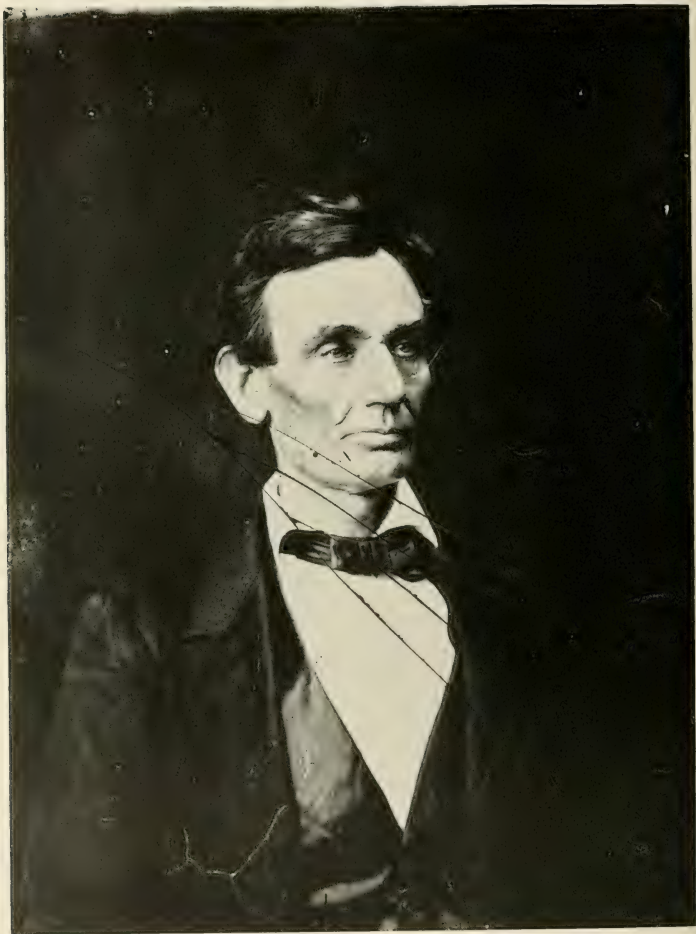
Plates 1 and 2 show prints made directly from the negatives. In plates 3 and 4 the lines of breakage and other imperfections have been eliminated by a skillful artist. It will be noted that in these pictures Lincoln is shown as smooth-shaven. It is reported that in October 1860 a letter was written to Mr. Lincoln suggesting that he grow a beard—advice that he seems to have followed, since he wore one on his inauguration the following March. Apparently, therefore, these negatives were made soon after the election of the previous November.

As stated above, according to report Lincoln considered these pictures as among the best made of him at the period. Fortunately the damage to the plates has not destroyed the likeness, as may be seen from the accompanying illustrations. These negatives form an important addition to the many treasures of the collections of the United States National Museum.



ORIGINAL NEGATIVE OF ABRAHAM LINCOLN AS RECEIVED FROM THE  
POST OFFICE DEPARTMENT

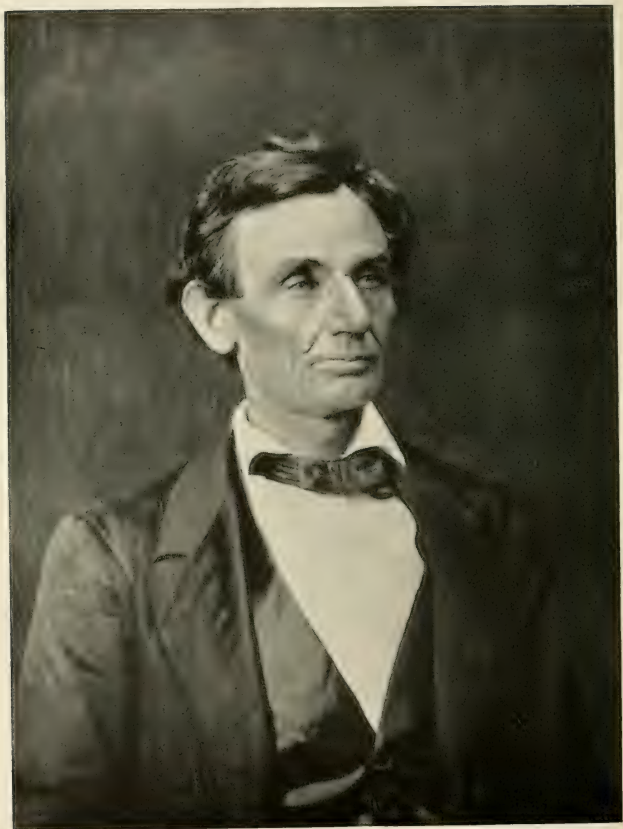




ORIGINAL NEGATIVE OF ABRAHAM LINCOLN AS RECEIVED FROM THE  
POST OFFICE DEPARTMENT



RETOUCHED PRINT FROM NEGATIVE SHOWN IN PLATE 1



RETOUCHED PRINT FROM NEGATIVE SHOWN IN PLATE 2

SMITHSONIAN MISCELLANEOUS COLLECTIONS

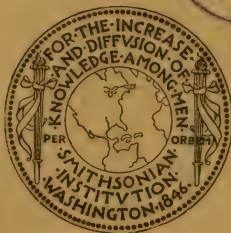
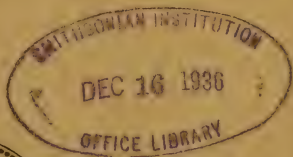
VOLUME 95. NUMBER 19

# CYCLES IN TREE-RING WIDTHS

BY

C. G. ABBOT,

Secretary, Smithsonian Institution



(PUBLICATION 3402)

CITY OF WASHINGTON  
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## CYCLES IN TREE-RING WIDTHS

By C. G. ABBOT

*Secretary, Smithsonian Institution*

In my paper "Solar Radiation and Weather Studies"<sup>1</sup>, I showed that the variation of the sun's emission of radiation since 1920 is the summation of at least 12 periodicities ranging from 7 months to 23 years in length. All of them are approximately, perhaps exactly, aliquot parts of 23 years. Hence, 23 years is a cycle wherein we might expect the weather and things dependent on it would show marked recurring features. Furthermore, although hitherto mathematical analysis has not disclosed why the sun's radiation should exhibit a fundamental and many overtones like a violin string, yet since observations show that it does so, it may well be that the fundamental is not 23 years, but 46, 92, or some other multiple of 23 years.

In my paper just cited I went on to show that all of the solar periodicities are also found in weather records of six stations (one of them, Adelaide, Australia, by the way) during the past century. Moreover, the 23-year cycle is to be found in varves of glacial age, in widths of tree rings in California and the West, in the levels of lakes and rivers, in the weather of the United States, and in other phenomena. It proved also that in many phenomena, and notably so in the levels of the Great Lakes and in the associated droughts in the Northwest, the 46-year cycle is predominant.

Recently Prof. C. J. Lyon, of Dartmouth College, has published a paper<sup>2</sup> on his measurements of widths of tree rings at six localities in Vermont and New Hampshire. My attention was particularly drawn to his figure 3, wherein he plots the average results through the whole range of time they cover. The locality Fairlee, Vermont, has the longest record, extending from 1544 to the present time, almost four centuries. Having graduated a slip of paper in 23-year intervals, I thought I could see in Professor Lyon's diagram a well-marked cycle of variation of this period throughout the entire series.

Professor Lyon has been so kind as to send me his original observations on the trees at Fairlee, and has graciously consented to let me

<sup>1</sup> Smithsonian Misc. Coll., vol. 94, no. 10, 1935.

<sup>2</sup> Ecology, vol. 17, no. 3, July 1936.

publish a statement of my reduction of them from the point of view of the 23-year cycle.

In the first place, the range of tree-ring widths is very great. After 1800, the widths as measured averaged several times as great as from 1544 to 1720. Hence for a fair comparison I thought it necessary to first approximately reduce all the data to a common scale. That such a reduction might not introduce a deformation of any 23-year cycle, I made the reductions at intervals which were in every case multiples of 23 years after 1544. The factors employed were as follows:

Interval .....	1544-1727	1728-1796	1797-1842	1843-present
Reduction Factor.....	1.0	0.8	0.4	0.3

With these changes the resulting mean tree-ring widths from Professor Lyon's measurements for Fairlee, Vermont, are as shown in table 1.

The values are arranged in 17 successive cycles of 23 years each. At the head of each column stands the first year of the cycle, so that the dates corresponding to all values may readily be obtained.

It was soon noted that every fourth cycle, the 1st, 5th, 9th, 13th, and 17th, differed decidedly in type from the average form of the others. This is but to say, of course, that there is a pronounced 92-year cycle in the tree-ring widths. It was noted, too, that five of the cycles, some belonging to the group just mentioned, some to the majority group, were partly intermediate between this type and the prevailing type of the 23-year cycle fixed by the remaining twelve cycles. These of intermediate type are the 2d, 7th, 9th, 10th, and 13th. Columns 18, 19, and 20 of the table give the mean forms of the three types just described. They are shown graphically in figure 1, C, A, B.

The range in widths of the prevailing mean form is about 50 percent, and that of the 92-year type about 70 percent, as based in each case on the smallest mean values. A large difference in average widths also distinguishes the two types. The average width for the mean of the five cycles (curve C) is 0.41 and that of the mean of the twelve (curve A) is 0.50, a range of 22 percent.

I have also sought to discover a periodicity of 46 years in the tree-ring widths for Fairlee. For this purpose the values were arranged in eight columns of 46 successive years each. The last column ends with the year 1911. It was soon noted that the columns alternately revealed forms of contrasting types. In figure 1, D, E, I show the mean form of the odd-numbered 46-year cycles in the lower curve, and the

TABLE I.—23-Year Periodicities

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	to	Mean of 1-5-9-13-17	Mean of 2-4, 6-8, 10-12, 14-16	Mean of 2-7-9-10-13
1544	1567	1590	1613	1636	1659	1682	1705	1728	1751	1774	1797	1820	1843	1866	1889	1912	4.2	4.2	4.4
1566	1589	1612	1635	1658	1681	1704	1727	1750	1773	1796	1819	1842	1865	1888	1911	1934	4.6	4.6	4.7
2.4	2.4	3.0	5.4	6.0	4.0	4.2	3.6	5.6	5.8	4.8	2.9	3.8	3.1	6.1	6.4	3.4	4.2	4.2	4.4
2.4	3.0	4.2	4.8	6.0	3.6	4.2	5.4	6.6	6.2	5.8	2.2	3.6	4.4	5.8	7.6	4.3	4.6	4.6	4.7
4.2	3.6	3.0	4.8	7.0	2.9	4.8	4.2	6.7	5.8	5.6	2.4	4.3	4.1	5.1	6.7	3.8	5.2	4.4	5.0
4.8	3.0	3.0	6.1	4.8	2.3	4.8	3.7	7.7	5.8	7.7	2.8	5.2	3.2	3.2	7.3	4.4	5.4	4.3	5.3
3.6	3.7	3.6	4.8	3.7	2.6	4.8	4.8	6.6	5.3	6.8	3.6	4.8	3.3	5.0	7.0	5.5	4.8	4.4	5.0
3.6	3.6	3.6	4.3	3.6	3.7	4.8	3.2	6.6	7.2	5.8	4.2	4.5	5.2	4.7	5.0	3.7	4.4	4.6	5.3
3.6	3.7	3.6	6.0	4.8	3.0	4.8	4.2	7.7	6.6	7.7	4.0	3.5	4.5	3.8	4.4	2.6	4.4	4.6	5.3
1.2	4.8	4.7	4.8	4.8	2.5	5.4	5.0	6.7	5.3	6.6	3.4	5.0	2.2	3.2	5.0	3.7	4.3	4.1	5.4
2.4	4.8	5.4	5.7	4.0	3.5	5.0	3.0	6.6	6.7	6.8	4.6	5.3	7.1	5.2	5.7	2.6	4.2	5.1	5.7
2.4	6.0	3.7	4.8	2.4	3.6	3.6	4.7	7.7	7.7	6.2	3.4	4.2	5.6	5.3	7.8	4.7	4.3	5.4	5.8
2.4	6.0	5.0	6.0	2.4	3.6	4.8	5.4	7.2	6.7	5.8	5.3	4.8	4.5	4.6	4.4	3.9	4.1	5.2	5.9
1.8	6.0	4.2	6.0	3.6	2.5	5.4	3.2	6.2	5.6	6.6	5.1	4.9	4.2	3.8	3.8	2.8	3.9	4.6	5.6
2.8	3.6	6.0	8.4	3.1	5.4	4.3	5.0	6.7	6.2	8.6	5.8	4.1	4.9	5.6	4.3	3.8	4.1	5.4	5.0
2.8	4.2	6.0	9.6	2.4	4.8	6.0	6.6	4.8	7.7	8.2	6.2	5.5	6.4	4.5	6.7	4.0	3.9	6.5	5.6
2.5	5.0	5.4	7.2	2.4	5.4	5.4	6.0	5.8	5.3	8.2	7.4	5.8	6.2	6.6	6.5	3.9	4.1	6.1	5.5
2.5	4.7	4.8	6.6	3.2	6.6	4.8	6.0	4.0	4.0	6.8	6.8	4.0	6.2	4.5	4.8	4.2	3.6	5.0	4.3
4.8	3.7	4.2	7.0	3.6	5.4	4.8	7.3	5.3	3.8	5.3	4.9	3.0	4.3	6.0	4.4	4.6	4.3	5.1	4.1
3.6	3.0	3.7	7.0	3.6	6.0	4.0	5.4	5.3	3.8	4.8	5.5	3.0	5.5	4.3	4.3	4.8	4.1	5.1	3.8
3.6	3.7	4.8	5.0	4.2	6.0	3.0	3.6	5.3	5.8	4.3	6.6	4.5	5.0	4.6	3.7	2.6	4.0	4.0	4.5
3.6	2.4	4.8	4.8	2.5	6.6	4.2	6.0	5.3	4.8	5.8	5.4	3.2	4.4	3.7	3.7	1.8	3.3	4.8	4.0
3.6	2.4	5.4	4.8	4.7	4.2	4.2	6.0	3.8	5.8	5.6	5.2	3.6	5.9	5.0	3.1	2.0	3.5	4.7	4.0
3.6	3.0	4.8	5.4	3.6	6.0	4.2	7.0	3.8	5.8	5.8	4.6	3.4	4.7	4.6	3.8	1.4	3.2	5.0	4.0
3.0	3.6	4.8	4.0	2.5	6.0	3.5	7.0	4.8	5.8	5.8	4.7	5.4	4.3	4.9	2.6	1.1	3.4	4.8	4.6

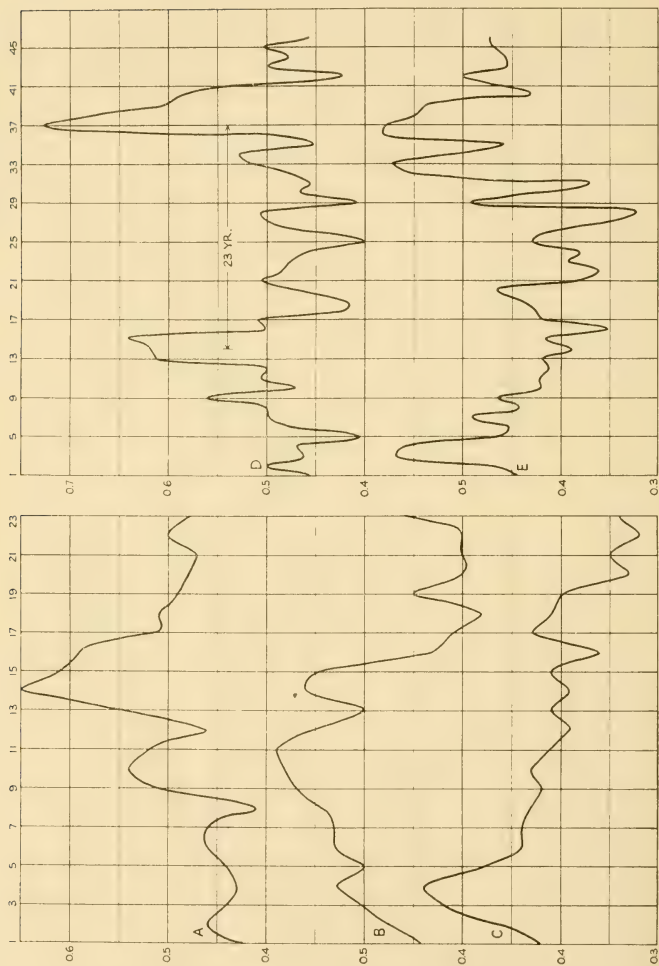


FIG. 1.—Cycles of 23, 46, and 92 years in tree-ring widths, Fairlee, Vermont.

A, the usual 23-year cycle, mean of 12 recurrences. B, an intermediate form of 23-year cycle, mean of 5 recurrences. C, the 23-year cycle which occurs once each 92 years, mean of 5 recurrences. D and E, alternate forms of the 46-year cycle. Each is the mean of 4 recurrences which occur in regular alternation in these contrasting forms. The 23-year cycle shown in D therefore confirms the 92-year cycle shown in C.

mean form of the even-numbered 46-year cycles in the upper curve. It will be observed at once that they differ in that the upper curve shows a strong 23-year cycle additional to that of 46 years, while in the lower curve this feature is missing. This, of course, is but to emphasize the fact already brought out above, namely, there is a strong 92-year cycle besides those of 23 and 46 years.

I suspect that meteorologists are rather inclined to distrust the origin and existence of the 23-year cycle which was indicated in my former paper as arising from the variability of solar radiation and expressing itself in weather and many phenomena depending thereon. Their hesitation is no doubt due to the smallness of the percentage and the absence of a theory of the solar variations, and to the reversals of phase which occur in the terrestrial manifestations of the subordinate solar periodicities, as strikingly illustrated in figures 16 and 17 of my paper "Solar Radiation and Weather Studies". I have still nothing to offer but statistical proofs of the important influences of the many periodicities integrally related to 23 years, but I feel somewhat supported in my conclusions by the recent paper of E. A. Cornish<sup>3</sup> on the precipitation at Adelaide, Australia, and the unreserved acceptance of this period as real by Dr. F. J. W. Whipple while he criticized the method of Mr. Cornish in presenting it.

In closing, I may draw attention to an important inference from this study of Professor Lyon's measurements of the tree-ring widths at Fairlee, Vermont. The 46-year cycle seems to be clearly in evidence since the year 1544, and covering eight recurrences of it. Counting back from the year 1911 when the eighth cycle ends (see curve D, fig. 1), we find that the low phase, corresponding no doubt to deficient water supply, ended about 1896. Now referring to figure 26 B of my paper "Solar Radiation and Weather Studies", the low phases of Lakes Huron and Erie also ended about 1896, and also 46 years previously thereto, at the ends of the great droughts of the forties and the nineties of the nineteenth century in our Northwestern States. Does not this long-continued series of 46-year precipitation cycles at Fairlee plainly warn us of the probable recurrence of a major drought beginning soon after the year 1975, and lasting about 10 years?

<sup>3</sup> Quart. Journ. Roy. Met. Soc., vol. 62, p. 481, 1936.



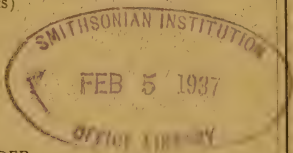


SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 20

# INACTIVATION OF PLANT GROWTH SUBSTANCE BY LIGHT

(WITH TWO PLATES)



BY

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AND

EARL S. JOHNSTON

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(WITH TWO PLATES)

## INTRODUCTION

The influence of general illumination upon the size and form of plants, as well as the induction of phototropic curvatures by unilateral light, has been explained in recent years on the basis of special growth substances. Since rate of growth is proportional to the concentration of growth substance (auxin) within certain limits (Went, 1928; Nielsen, 1930; Söding, 1936; cf. Boysen Jensen, 1936 a), differential distribution of these growth-regulating substances should be expected to result in unequal enlargement of the constituent parts of a growing tissue or organ. The commonplace bending of plant shoots toward light incident from one side has been ascribed to the unequal distribution of growth-promoting substance on the illuminated and shaded sides. More growth substance occurs on the shaded than on the illuminated side, hence the rate of elongation in this region is relatively greater, and the organ is forced to bend.

The precise manner in which light influences the role of growth substances in a growing plant is not easy to explain. Light may modify the quantity of growth substance present by photo-formation or -destruction. The extent to which translocation and effective action of growth substance are influenced also constitutes an important aspect of the problem. Various investigations up to the present have emphasized the effects of light upon movement and activity of growth regulators, especially in relation to phototropic phenomena; on the other hand, photo-synthetic and -destructive reactions have not received sufficient attention. For an extensive dis-



cussion of the growth substance literature the reader should consult Boysen Jensen's (1936a) English translation of "Die Wuchsstofftheorie."

The studies recorded in this paper attempt to show whether the function of light in phototropism and morphogenesis is primarily concerned with the redistribution of plant growth substance (hormone), or with its inactivation.

### MATERIALS AND METHODS

The following plant materials were used in the experiments: Seedlings of *Avena sativa*, varieties Victory and Markton; seedlings of *Zea mays*, a sugar endosperm type known as Connecticut No. 2; and terminal shoots of young *Nicotiana tabacum*. The oat seeds were supplied through the kindness of Mr. T. Ray Stanton and the tobacco plants by Dr. J. E. McMurtrey, Jr., United States Department of Agriculture, Washington, D. C. The seedlings were grown in a darkroom operated at 80° F. and 90 percent humidity. Only phototropically inactive orange-red light (Wratten Safelight Series O) was used to facilitate making the various necessary manipulations. A water-culture technique modified after the method of F. W. Went (1928) was used for growing the oats. Corn seedlings were grown in sandy soil contained in clay pots.

Apparatus for the water cultures is illustrated in plates 1 and 2. The portable tray shown in plate 2 proved to be very convenient in carrying out the various experiments. The essential parts of this tray are a wooden frame, waterproofed with paraffin, phosphor-bronze spring clamps, glass holders, and a Pyrex glass water cell designed to accommodate the roots of 10 oat plants. Paraffined zinc water cells were used in a few supplementary experiments. Distilled water was used in all these cells. As may be seen in plate 1, the glass holders were made with care so as to hold the oat seeds firmly and permit an ample portion of the sprout to project through and above the glass collar. The diameter of rod, and size and tension of the spring clamps were standardized so as to permit exchangeability and easy adjustment of position in the racks. Thus the technique becomes practically free from objectionable features so that uniform test plants may be obtained repeatedly.

Seedlings of *Avena* were grown as follows: Seeds with the chaff removed and selected for uniform size were soaked in distilled water for 4 hours, and then placed each with the grooved side down about one-half inch apart on moist filter paper in petri dishes. They

were exposed to moderately bright skylight for 5 hours (to keep the first internode short during subsequent growth) and then transferred into the darkroom for the rest of their development. Some 48 hours after the first soaking in water, the seedlings were placed in glass holders and the coleoptiles allowed to grow vertically straight in the humid darkroom for 30 hours. Then the seedlings were selected for size and straightness and arranged in uniform racks. In 75 to 80 hours from the beginning of germination the coleoptiles attained about two-thirds their final size and were ready for use.

Maize seeds were soaked in water for 4 hours and then put to germinate in moist soil in the darkroom. About 100 to 120 hours were required to obtain maize coleoptiles two-thirds their final size, and suitable for experimentation.

The *Avena* test plants were decapitated 40 minutes before they were to be used in the biological assay of growth substance. Small pieces of plant tissue or agar blocks containing unknown amounts of the substance were tested by applying them unilaterally to the cut surfaces of the coleoptile stumps. Growth curvatures at the end of 2 hours were recorded as shadow pictures on photographic paper (pl. 2, lower), and later the angles were measured with a protractor. The average *Avena* curvature in degrees is recorded in the tables of data.

The sources of radiation employed were a mercury in quartz arc operating on 220 volts D. C., and a Mazda 60-watt tungsten lamp run on 110 volts A. C. White light from the arc, designated as "total arc" in the tables, was filtered through 5 cm of distilled water contained in a glass cell in order to remove short ultraviolet and long infrared wave lengths. The blue mercury line, 4358 Å, was isolated with Corning glass line filter no. 7, 3.06 mm and 3.25 mm thick, in addition to the water filter. Ultraviolet radiation from the mercury arc was passed through only a no. 986 Corning red-purple Corex "A" filter 7 mm in thickness. Excised coleoptile tips and agar blocks during exposure were kept in moist glass chambers lined with wet blotting paper. When ultraviolet rays were used, thin quartz covers were placed over the moist chambers to permit entrance of short wave lengths. With the Mazda lamp, no filters were used except the 3-mm-thick glass wall of the moist chamber, which removed some infrared rays.

In each case the energy incident upon the plants was measured with a thermocouple and galvanometer calibrated with a standard lamp. Radiation from the arc was allowed to fall vertically through the appropriate filters directly upon the plant materials shielded from

other light in a suitable box. For lateral radiation a plane mirror was employed at an angle of  $45^\circ$  to reflect a horizontal beam onto the plant parts maintained always in an erect position during the experiments.

## EXPERIMENTATION

### INFLUENCE OF GENERAL RADIATION UPON GROWTH SUBSTANCE IN COLEOPTILE TIPS

*Avena sativa*.—Intact coleoptiles growing in water cultures were subjected to radiation vertically incident upon the tips for different lengths of time, while control plants of the same size were kept in

TABLE I.—*Influence of Mercury Arc Radiation on Growth Substance*  
Intact tips illuminated vertically (*Avena*)

Date 1936	Character of radiation			Material radiated	No. of tests	Avena curvature (degrees)	
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Treated	Dark control
Aug. 13	4358A	278	55	Victory	8	11.0	10.9
25	"	"	180	"	10	9.5	....
	"	"	300	"	10	8.7	....
14	Total arc	15080	120	"	10	3.3	11.0 <sup>a</sup>
19	" "	"	135	"	10	2.3	5.5 <sup>b</sup>
20	" "	"	120	"	10	4.3	10.9
21	" "	"	"	"	10	2.4	11.7
31	Ultraviolet	1888	"	Markton	10	1.1	....
27	Total arc	15080	135	"	8 (from tips)	2.6	....
	" "	"	"	"	8 (from bases)	0.3	....

<sup>a</sup> 9 tests made.

<sup>b</sup> 8 tests made.

NOTE.—In all tables total arc refers to that portion of the mercury arc radiation transmitted by glass and 5 cm water.

darkness. Immediately following the period of irradiation, apical 3-mm portions were excised from the plants, and these were placed unilaterally (with a little 5 percent gelatin) upon decapitated *Avena* test plants. Darkened control tips were tested in a similar manner.

The blue mercury line, 4358 Å, was used to illuminate different sets of intact plants for 55, 180, and 300 minutes. Resulting curvatures of the test plants showed only small and perhaps insignificant differences in growth substance in these irradiated tips as compared with the darkened controls (table I).

Intense light from the total arc filtered through glass and 5 cm of water was used in the same manner as stated for the blue light. In this light, growth substance content of the tips was reduced appreciably by exposure for 120 minutes (table I). Averages for four

separate series showed a curvature of 9.8 degrees produced by control tips, while illuminated tips yielded only 3.1 degrees. Ultraviolet irradiation for 120 minutes reduced the curvature to 1.1 degrees. Another experiment performed August 27 with light from the total arc indicated that the normal quantity of growth substance contained in the tips of darkened plants is not driven downward into lower levels of the coleoptile during radiation. At a level 1.5 cm below the tip there was no increase in growth substance commensurate with the marked decrease at the tip caused by illumination.

A series of experiments was performed to determine whether illumination might reduce the amount of growth substance contained in excised coleoptile tips. The tips were excised with a razor blade, and after being moistened on the cut surface with a small amount of 5 percent gelatin, they were placed upon a clean glass plate in a petri dish lined with wet filter paper to prevent desiccation. Tips were irradiated in these dishes for different lengths of time, and excised control tips of each series were allowed to stand in darkness for the same time as the exposed tips (table 2). Irradiation for 60 or 120 minutes clearly reduced the amount of curvature obtained in the tests with *Avena* stumps. Seven series of experiments with both Victory and Markton varieties of oats treated for 120 minutes with radiation of approximately 13,000 and 15,000 ergs/cm<sup>2</sup>/sec. show an average value of 3.8, while the value for the dark controls is 7.0. In other words, irradiation reduced the growth substance content of isolated tips to less than half the content of those kept in darkness for the same time. Ultraviolet treatment for 60 minutes on August 24 and 31 (table 2) also reduced the growth substance appreciably.

A study of the growth substance content of excised Victory oat tips in relation to exposure time (the intensity being constant) was made on August 22. Disappearance of growth substance was proportional to the exposure period; two hours of light reduced the curvature to 3.2 as compared with dark controls of 9.5. On September 18 an intensity series was studied, and here again greater destruction was indicated with increasing dosage of radiation (table 2).

*Zea mays*.—Experiments with excised coleoptile tips of maize were carried out in several different ways. On September 12 and 13, excised tips each 4 mm in length were placed individually in a vertical position upon small blocks of 3 percent agar measuring 1×1.5×1.5 mm. Some were placed in the light, others kept in darkness for 120 or 240 minutes during the period of diffusion of growth substance into the agar. At the end of the diffusion periods

TABLE 2.—*Influence of Mercury Arc Radiation on Growth Substance*  
Excised tips illuminated vertically (*Avena*)

Date 1936	Character of radiation			Material radiated	No. of tests	Avena curvature (degrees)	
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Treated	Dark control
Aug. 24	Ultraviolet	1888	60	Victory tips	10	3.9	9.8
	Total arc	15080	120	" "	10	3.5	....
31	Ultraviolet	1888	60	" "	10	2.5	9.7 <sup>a</sup>
19	Total arc	15080	120	" "	10	4.7	6.2
20	" "	"	"	" "	10	3.8	7.6
21	" "	"	"	" "	8	0.8	4.6 <sup>a</sup>
Sept. 16	" "	12784	"	Markton tips	17	6.2	9.7 <sup>b</sup>
Aug. 22	" "	15080	30	Victory tips	10	9.3	9.5
	" "	"	60	" "	10	5.7	....
	" "	"	120	" "	10	3.2	....
Sept. 18	" "	254	"	Markton tips	12	10.5	12.1
	" "	1128	"	" "	12	10.3	....
	" "	12784	"	" "	12	4.5	....

<sup>a</sup> 9 tests made.

<sup>b</sup> 16 tests made.

TABLE 3.—*Influence of Mercury Arc Radiation on Growth Substance*  
Excised tips illuminated vertically (*Zea mays*)

Date 1936	Character of radiation			Material radiated	No. of tests	Avena curvature (degrees)	
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Treated	Dark control
Sept. 12	Total arc	12784	120	Tips on agar	6 agar applied	8.8	15.2
13	" "	"	240	Tips on agar	6 agar applied	7.8	18.8
12	" "	"	120	Tips on glass	6 tips applied	6.5	14.8
	" "	"	"	Tips on glass	8 half tips applied	4.8	10.8 <sup>a</sup>
17	" "	"	"	Tips on glass	24 half tips applied	2.1	13.1 <sup>b</sup>
14	" "	"	120 (plus 120 min. dark)	Tips on glass	24 half tips applied	2.1	....
	" "	"	(120 min. dark plus) 120	Tips on glass	24 half tips applied	2.5	....
	" "	"	240	Tips on glass	24 half tips applied	0.0	....

<sup>a</sup> 10 half tips applied in test.

<sup>b</sup> 22 half tips applied in test.

stated, the agar blocks were applied unilaterally to *Avena* stumps. The curvatures obtained in this way were markedly reduced by light treatment (table 3).

Similar reduction in active growth substance was obtained by exposing to light excised tips placed on glass slides in moist petri dishes (table 3). Whether the whole tips or split half tips were applied (with a little gelatin) to *Avena* stumps, light reduced the curvature to less than half that given by tips maintained in darkness. Furthermore, an exposure of 240 minutes produced still greater loss of growth substance than did the exposures lasting for 120 minutes.

In experiments on September 14, one set of 12 excised tips was illuminated for 120 minutes, then kept in darkness 120 minutes, another set of 12 was kept darkened 120 minutes, then illuminated 120 minutes, and a third set of 12 was illuminated 240 minutes. About the same small curvature (2.1 and 2.5 degrees) was obtained with 120 minutes of radiation irrespective of whether 120 minutes of darkness came before or after the light treatment. On September 17, 12 tips irradiated for 120 minutes and directly applied to test plants yielded 2.1 degrees curvature, while the dark controls gave 13.1. In the experiments of September 14, 240 minutes of irradiation reduced the growth substance to zero.

In summarizing, it would appear that radiation above certain minimum quantities in the ultraviolet and visible regions of the mercury arc spectrum causes a decrease in amount of growth substance that can be obtained from intact and excised coleoptile tips of *Avena* and *Zea*.

#### INFLUENCE OF UNILATERAL RADIATION UPON GROWTH SUBSTANCE IN COLEOPTILE TIPS

*Avena sativa*.—Intact coleoptiles were irradiated from one side for various lengths of time. During this irradiation the plants were oriented in specially constructed glass holders so that the direction of the light beam was through the longer transverse axis—that is, one of the narrow edges of the coleoptile was illuminated. Curvatures occurred toward the light. At the end of the period of light exposure the tips were excised and split vertically into halves which then were applied unilaterally with gelatin to *Avena* stumps. In all cases the half tips near the light produced slightly greater curvatures than did those on the shaded side (table 4). This same table also indicates that lateral light does not cause increased accumulation of growth substance below the tip when the amount obtained from the tip is lowered.



In order to obtain further information concerning the distribution of growth substance in the lighted and shaded portions of unilaterally illuminated coleoptiles, two series of excised *Avena* tips 3 mm in length were used. The tips were split at the bottom and placed erect upon a thin glass microscope cover slip supported in a paraffin block (fig. 1). Small 3 percent agar blocks were attached with 5 percent gelatin to each bottom half of each tip so that one vascular bundle was in contact with each block. One experiment included 12 tips irradiated with an intensity of 5700 ergs/cm<sup>2</sup>/sec. In another, 13 tips were irradiated with 278 ergs from one side, the exposure time being

TABLE 4.—*Influence of Mercury Arc Radiation on Growth Substance*  
Intact tips illuminated laterally (*Avena*)

Date 1936	Character of radiation			Material radiated	No. of tests	Avena curvature (degrees)	
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Near	Far
Aug. 26	4358A	252	75	Markton	20 half tips applied	4.5	3.1
	"	"	60	"	20 half tips applied	4.6	3.1
	"	"	35	"	20 half tips applied	3.7	2.5
27	Total arc	12320	75	"	16 half tips applied	5.4	2.3
31	" "	"	1 (plus 30 min. dark)	"	10 half tips applied	2.6	2.8
27	" "	"	120	"	4 (from tips) 4 (from bases)	4.5 0.8	

120 minutes. During this 120-minute period, growth substance moved into the agar blocks in contact with the basal cut ends. These blocks, which acquired growth substance from the illuminated and shaded half tips, were applied then to test plants, alternating "near" and "far" blocks along the rack of *Avena* stumps. In both series, more growth substance was recovered from the side farther away from the light (table 5).

*Zea mays*.—In a manner similar to that employed with *Avena* tips experiments were performed with excised tips of *Zea*. These data are also given in table 5. Here again less growth substance was recovered from the side near the light, and, indeed, less from the far side than from coleoptile half tips treated in exactly the same way but maintained in darkness for the 120-minute period of diffusion.

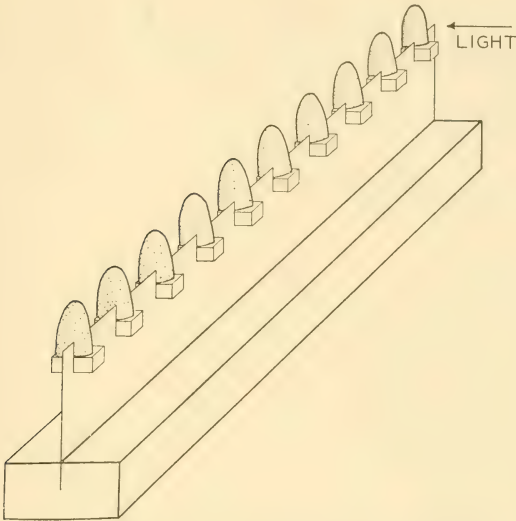


FIG. 1.—Method of diffusing growth substance into agar blocks from split coleoptile tips illuminated unilaterally.

TABLE 5.—*Influence of Radiation on Growth Substance*  
Excised tips illuminated laterally (*Avena* and *Zea mays*)

Date 1936	Character of radiation			Material radiated	No. of tests	Avena curvature (degrees)		
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Near	Far	Dark control
Sept. 16	Total Hg arc	5700	120	Markton tips split on agar	24 agar blocks applied	3.5	6.7	...
18	Total Hg arc	278	"	Markton tips split on agar	26 agar blocks applied	1.6	5.8	...
11	Total Mazda	752	"	Zea tips split on agar	22 agar blocks applied	5.4	8.9	...
17	Total Hg arc	10480	"	Zea tips split on agar	22 agar blocks applied	9.6	12.9	14.7 <sup>a</sup>

<sup>a</sup>Average of 18 tests.

In summarizing, it may be said that lateral radiation of *intact* coleoptiles of *Avena* causes marked reduction in the growth substance that can be obtained from the tips. Slightly more growth substance was recovered from the illuminated than from the shaded side. However, when *excised* tips of *Avena* and *Zea* are subjected to lateral illumination, less growth substance can be recovered from the side near the light. There is no indication of an increased growth-substance content on the shaded side, since the amount obtained was less than that of the control.

INFLUENCE OF LIGHT UPON GROWTH SUBSTANCE "DIFFUSED"  
INTO AGAR

Growth substance was obtained in agar blocks of half the standard size (Dolk and Thimann, 1932) by placing them in contact with the cut surfaces of *Nicotiana* shoots and *Zea* coleoptile tips. Each of these

TABLE 6.—*Influence of Mercury Arc Radiation on Growth Substance*  
Diffused into agar for 2 hours in darkness (*Nicotiana tabacum* and *Zea mays*)

Date 1936	Character of radiation			Material used	No. of tests with Markton	Avena curvature (degrees)	
	Wave length	Intensity (ergs/cm <sup>2</sup> /sec.)	Duration (min.)			Treated	Dark control
Sept. 12	Total arc	12784	130	<i>Nicotiana</i> and agar A	11	1.0	9.0
14	" "	"	120	<i>Nicotiana</i> and agar A	12	0.7	9.0
17	" "	"	"	<i>Zea</i> tips and agar A	12	12.6	16.8
29	" "	15080	"	<i>Nicotiana</i> and agar B	6	15.3	17.0*

\* 5 tests made.

blocks was cut into two approximately equal parts; then one part was kept in darkness, while the other was irradiated for 120 minutes. Then they were cut into small pieces, and the latter were applied to *Avena* test stumps. The data (table 6) for September 12 and 14 in which *Nicotiana* was used, indicate a remarkable inactivation of growth substance by the light treatment. With another brand of agar (probably much cleaner) obtained from a different manufacturer, there was less difference between the light-treated blocks and the controls, as shown in the data for August 29. Also, the difference was less with *Zea* growth substance than with that obtained from *Nicotiana*. In all cases, however, less growth substance curvature was obtained with the irradiated portions of the agar blocks than with the darkened control portions.

## DISCUSSION

The relation of light to growth substance activity in plants is not well understood, although considerable work has been done on various aspects of the problem. Apparently under certain conditions, light enhances the formation of growth substance; effective action of the substance is greater, however, in darkness than in light (Thimann and Skoog, 1934). An increase in the amount of growth substance due to light exposure has been reported for a number of plants by various workers. *Lupinus* seedlings subjected to weak Mazda light (Navez, 1933), *Raphanus* seedlings kept in the greenhouse (Van Overbeek, 1932), young *Nicotiana* in daylight (Avery, 1935), and *Vicia* growing in light (Thimann and Skoog, 1934), have been found richer in growth substance than similar control plants kept in darkness. The production of root-forming materials occurs in orange-red light, though their activity apparently is inhibited by light (Went, 1935). *Avena* coleoptiles and *Raphanus* hypocotyls exposed to light exhibit less response to given amounts of growth substance than darkened control plants (DuBuy, 1933; Van Overbeek, 1933).

Various theories have been proposed to explain the depressing effect of light upon growth. A change in the ability of cells to respond to growth substance may occur in light (Van Overbeek, 1933; cf. Boysen Jensen, 1936 a), or perhaps light hastens senescence (DuBuy, 1933). Laibach (1936) postulates the formation of an excitatory substance in darkened plant cells which furthers the action of growth substance. Absence of this cooperating stuff in illuminated tissues is supposed to account for the observed decrease in growth rates.

It is well known that decapitated *Avena* test objects possess all the requirements necessary for growth except growth substance. Experiments reported in the present paper indicate that the growth-promoting property of excised and illuminated coleoptile tips is decreased below the value of excised darkened tips when they are tested upon decapitated coleoptiles in darkness. Likewise, irradiated growth substance in agar blocks lost a large part of its activity. It appears, therefore, that growth substance itself, not some other material, is inactivated by irradiation in our experiments. Preliminary investigations by Navez (1936) indicate that photo-destruction of growth substance takes place through the photodynamic action of certain plant pigments.

Many of the instances on record concerning the more rapid growth of plants at night are explainable, perhaps, on the basis of growth-substance synthesis in the daytime and its increased effectiveness in

darkness. Spectrum sensitivity data obtained in studies on phototropism are in general accord with similar information about the formative influence of different wave lengths of light upon the growth of illuminated whole plants (cf. Burkholder, 1936; Duggar, 1936; Johnston, 1934). The formative action of light in relation to growth-promoting substances has been emphasized in a recent paper by Katunskij (1936). Students of phototropism at present usually explain differential growth under conditions of unilateral illumination as being a result of unequal growth substance concentration on the lighted and shaded sides. This concept, which had its origin many years ago, is supported by a considerable body of evidence (cf. Boysen Jensen, 1936a). The manner in which unequal distribution comes about is not agreed upon by all investigators.

Went's (1928) experiments with excised and unilaterally illuminated *Avena* coleoptile tips placed on agar blocks have seemed to indicate that the amount of growth substance given off by the lighted side is appreciably lessened, while that of the darkened side is slightly increased above the amount in tips kept in darkness. If the total amount recovered from unilaterally lighted tips is adjusted to 100, then 68 percent of this comes from the shaded side while 32 percent is recovered from the lighted side. Recalculation of Went's data in a different way shows an increase of only 7 percent in the shaded half tips as compared with similar half tips kept in the dark. Van Overbeek (1933) obtained evidence for cross transfer of growth substance (in some experiments, not in others) with *Raphanus* hypocotyl segments which were illuminated unilaterally. It seems certain now that less growth substance occurs in the illuminated half of an organ than in the shaded half during phototropic activity (Went, 1928; Van Overbeek, 1933; Boysen Jensen, 1933, 1936; cf. DuBuy and Nuernbergk, 1932-1935), but whether this difference always comes about by lateral displacement seems open to reasonable doubt.

Some investigators have reported decreased amounts of growth substance in tissues exposed to light. Went (1928) observed a decrease of 18 percent in *Avena* coleoptile tips which had been exposed to 1,000 meter candle seconds; various results were obtained with larger and smaller dosages of light where events were apparently complicated by modified rates of transport. Although weak blue light and even strong white light with the infrared and some red removed is reported to have no diminishing effect upon growth substance, DuBuy (1933) found that strong white light plus infrared decreased the supply in *Avena*, and direct sunlight eliminated it completely. It is of considerable interest that the effect of light upon growth response

depends upon the kind of growth substance present (Van Overbeek, 1936). When auxin *a* is applied unilaterally to *Avena* coleoptiles, curvature is less in light than in darkness, but when 3-indole acetic acid is used, the curvatures are the same in light and in darkness. Van Overbeek (1936 a) has reported, furthermore, that exposure to the red plus infrared radiation of an ordinary darkroom lamp causes a decreased growth substance content in the tips of *Avena*.

Experimental results reported here indicate marked decreases in growth-promoting properties of irradiated tissue and of agar blocks containing growth substance. When so great losses occur under the influence of controlled radiation as mentioned, it is not probable that translocation of the active material should play any prominent role in growth phenomena at the same time. Under some circumstances, e. g., low light intensity, it may be that more growth substance is *moved* than is *destroyed* in the plant. It appears from the experimental evidence presented in this paper that light of high intensities has a destructive or inactivating action on plant growth substance, which is of great importance for phototropism and morphogenesis.

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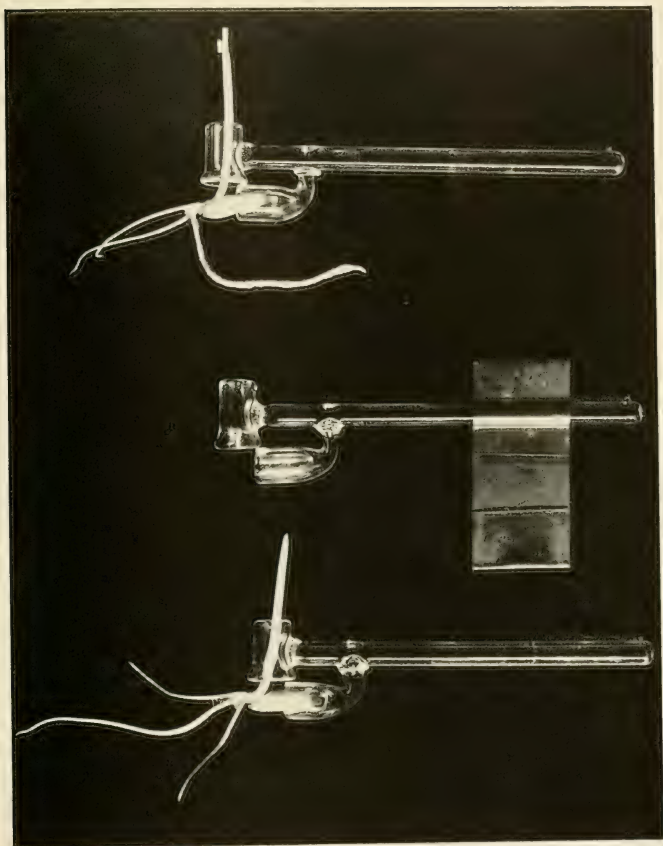
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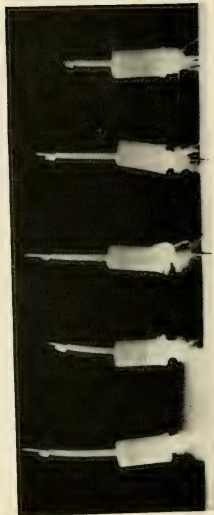
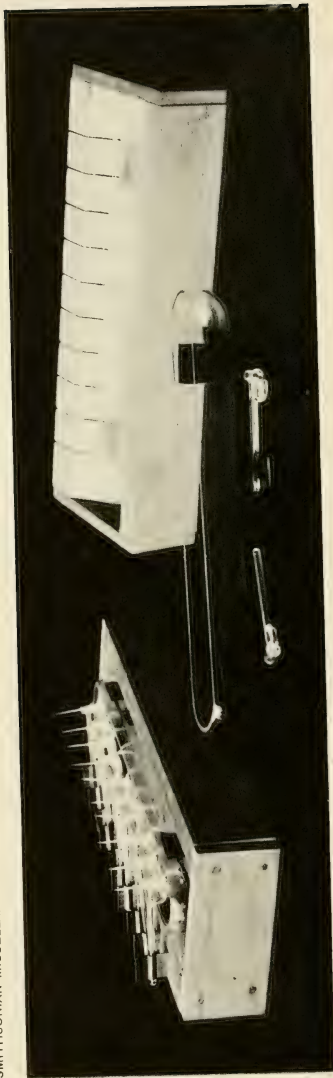
a. Glass *Avena* holders, showing position of seedling (lower), position of spring clamp (center) and general appearance of tip placed against protruding first leaf on decapitated stump (upper). Note: The small tip was displaced through an angle of  $90^\circ$  in order to be shown in the photograph.



b

b. A simplified type of *Avena* holder designed by L. B. Clark, of the Division of Radiation and Organisms, after the completion of the present studies.

## SMITHSONIAN MISCELLANEOUS COLLECTIONS



Upper figure, water-culture equipment for growing oat seedlings, showing on the right the wooden frame, V-cut to hold the glass water cell and slotted to hold the spring clamps with their glass holders, and, on the left, the assembled water-culture equipment, showing young oat seedlings in the small glass holders with their roots in water in the glass water cell.

Lower figure, shadow pictures from one experiment illustrating type of curvatures obtained from test plants in darkness with attached tips from dark control plants (left) and with tips from plants exposed to light (right). The greater amount of growth-substance activity is shown by the greater degree of curvature.

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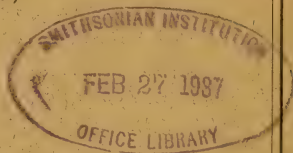
THE DEPENDENCE OF CARBON DIOXIDE ASSIMILATION  
IN A HIGHER PLANT ON WAVE LENGTH  
OF RADIATION

(WITH THREE PLATES)

BY

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By W. H. HOOVER

*Division of Radiation and Organisms, Smithsonian Institution*

(WITH THREE PLATES)

Growth in dry weight in autotrophic plants requires the absorption and assimilation of carbon dioxide from the air, and this is the basic physiochemical reaction of all life.

The problem of the effect of different wave lengths of light on the carbon dioxide assimilation by a plant has been the subject of investigation for many years. In most of the earlier investigations broad spectral regions were used, and not much attention was given to the distribution of energy in the various spectral regions. Thus, very little information may be obtained from these earlier investigations.

Among the first investigators to realize the importance of determining the distribution of energy in the spectral regions were Kniep and Minder (1909). They used sunlight during the middle of the day with glass filters to isolate the red and blue regions of the spectrum and a liquid filter for the green region. They came to the conclusion that red and blue light of the same intensity produced about the same rate of photosynthesis. Warburg and Negelein (1923), working with *Chlorella* suspended in solution and using a quartz mercury arc with line filters, reported that red light was the most efficient in producing photosynthesis, and blue light the least. In their experiment they assumed complete absorption of the light.

On the basis of equal energy absorption, Burns (1933) and Gabrielsen (1935), working with higher plants, both draw the conclusion that red light is the most efficient in producing photosynthesis, green next, and blue light the least. They both used rather broad spectral regions and obtained values for only a few regions of the spectrum. It is also not clear from their data that they obtained a true measure of the absorbed energy.

The purpose of the present investigation is to determine the rate of photosynthesis as a function of the wave length of light on the basis of equal values of incident radiation.

## APPARATUS

The apparatus used in this experiment has been described in a paper by Hoover, Johnston, and Brackett (1933). Although the apparatus was rebuilt in order to improve the method of controlling the temperature and humidity, its general features remain the same. The plants are placed in a closed glass system in which a rapid recirculation of air is maintained. New air at a constant rate enters the system at one point and is drawn off at another for analysis.

The design of the glass which holds the nutrient solution was changed in order to permit a continuous flow of solution. The seal between the flask, holding the plant, and the growth chamber was made by the lower part of the growth chamber dipping into a cup of paraffin oil sealed to the neck of the flask. A view of the apparatus is shown in plate 1.

## FILTERS

The problem of obtaining radiation of sufficient energy in narrow wave-length bands over an area large enough for even a small wheat plant is a difficult one. A good monochromator gives the best means of obtaining narrow bands, but in most cases the radiation intensity is low except for very small areas. Glass, liquid, or dyed gelatin films may be used to obtain bands of radiation of considerable intensity over a large area, but these filters transmit rather broad bands. Thus it is difficult to compare the results obtained with these filters. There are, however, certain combinations of these filters called line filters which do transmit narrow bands of radiation. The transmission of these filters is low, but when used with line sources such as the mercury arc, sufficient energy was obtained for this experiment. The following filters were used to isolate a few of the strong mercury lines.

Wave length (A)	Filter			
5780.....	Corning	monochromatic	filter	No. 4
5461.....	"	"	"	" 5
4358.....	"	"	"	" 7
4048.....	"	"	"	" 8
3650.....	"	"	"	" 10

The Christiansen filter described by McAlister (1935), although not an ideal filter, has certain advantages for an experiment of this nature. By merely changing the temperature of the filters it was possible to cover the entire spectral region of photosynthesis by using two filters with different proportions of carbon disulphide and benzene. In the first experiment with these filters, four filters 6 inches in

diameter and 2 inches thick were used in order to illuminate the plants on four sides. The temperature of the filters was controlled by placing them in thermostated water baths. A very simple optical system was used in this case. A 1000-watt Mazda lamp was placed near the focus of a concave mirror in order to obtain a magnified image of the source at the plant. The light passed twice through the filter before reaching the plant. Figure 1 represents the energy distribution obtained with these filters under the condition of the experiment. The distribution of energy in the bands was not entirely satisfactory, owing

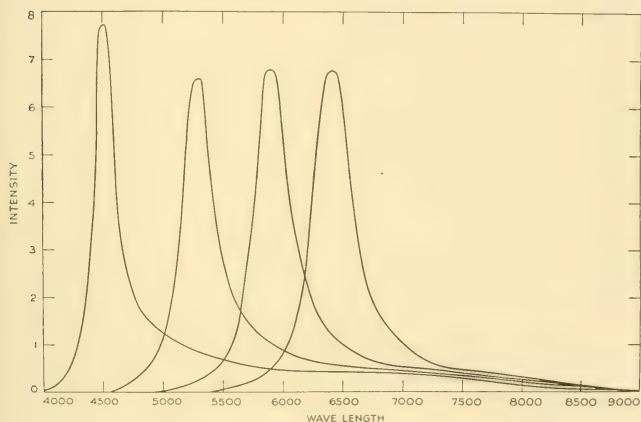


FIG. 1.—Energy transmission curves for 6-inch Christiansen filters.

to imperfections in the concave mirrors and to the fact that the filters were too thick to obtain good temperature control.

In the second experiment with the Christiansen filters sunlight was used as the source of radiation. Sunlight was obtained for the experiment by using a large coelostat located on the south side of the Smithsonian building. The moving mirror of the coelostat was 30 inches in diameter. Light reflected from this mirror was reflected by a second mirror to a third mirror located at one end of a long room. This mirror was about 60 feet from the plants. This combination of mirrors illuminated an area at the plant chamber about 15 inches in diameter. A Christiansen filter 12 x 14 inches and 1 inch thick was made in order to use most of the energy in this beam. The filter was placed 50 feet from the plant chamber. The distribution of energy in

the spectral bands obtained with this filter is represented in figure 2. These bands are much narrower than those obtained with the 6-inch filters. Plate 2 shows the large coelostat and plate 3 the large filter with water bath for controlling the temperature. In order to use the entire width of the beam of light, which was five or six times as wide as the growth chamber, a system of plane mirrors was used to reflect the light to the plants. This gave a fairly uniform illumination over the entire plant.

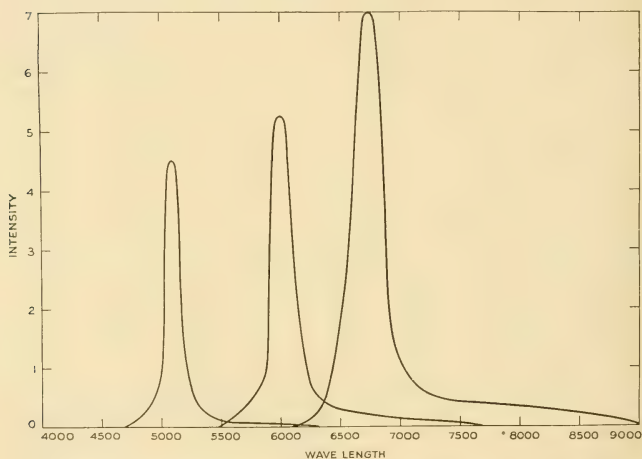


FIG. 2.—Energy transmission curves for the 12 by 14 inch Christiansen filters.

### EXPERIMENTATION

Wheat was germinated between layers of moist filter paper in a covered glass dish at a temperature of  $25^{\circ}\text{C}$ . When the roots had grown to a length of 2 or 3 cm, the young wheat plants were transferred to a germination net stretched over a glass dish through which tap water flowed. The plants were illuminated by a 200-watt Mazda lamp placed 30 cm above the netting. When the seedlings were approximately 4 or 5 cm in length, four individuals, selected for uniformity of size, were transferred to the growth chamber. The plants were supported by means of cotton in small holes in a paraffined flat cork stopper that fitted into the top of the flask of nutrient solution. The flask with the plant in place was then connected to the growth chamber in the manner explained above.

The plants were grown under controlled conditions for a few days before being used in an experiment. The temperature was about 21° C., humidity about 70 percent, carbon dioxide concentration two or three times that of normal air, the light intensity 1500 foot-candles for 18 hours a day, and the root temperature about 18° C. The plants were kept under these conditions except during the time observations were being made.

The light intensity obtained with the filters was never more than 300 foot-candles, the carbon dioxide concentration between two and three times that of normal air, and the temperature about 21° C. Under these conditions light was the limiting factor.

Using the quartz mercury arc and line filters, the ratio between the rate of photosynthesis at 5461 Å and 4350 Å remained about the same for the same plant on different days as well as for different plants grown under the same conditions. This furnished a means of comparing the results with various filters throughout the course of the experiment. 5461 Å was used as the standard, and the ratio of the rate of photosynthesis at 5461 Å and other wave lengths was determined.

In order to correct for respiration, the respiration rate was determined before and after each light observation, and appropriate corrections were applied to the photosynthetic rates observed.

## RESULTS

Measurements were made at various wave lengths of the photosynthesis produced in wheat by the rays transmitted by Christiansen filters adjusted to give predominantly these several wave lengths. In each case the measurements corresponded to equivalent intensities of radiation transmitted by the filters as determined by a thermocouple placed inside the growth chamber. The direct results obtained with these filters are given in table 1 and figure 3. Curve A represents the results obtained with the large Christiansen filters and sunlight, curve B those obtained with the 6-inch Christiansen filters and Mazda lights, and the points marked X are those obtained with the line filters and a quartz mercury arc.

The curves show two maxima of photosynthesis—one in the blue about 4400 Å, and the other in the red at 6500 Å. The green region of the spectrum was less effective. The maxima obtained with the large filters are somewhat higher than those obtained with the small filters, owing to the fact that the wave-length bands are narrower in the first case.



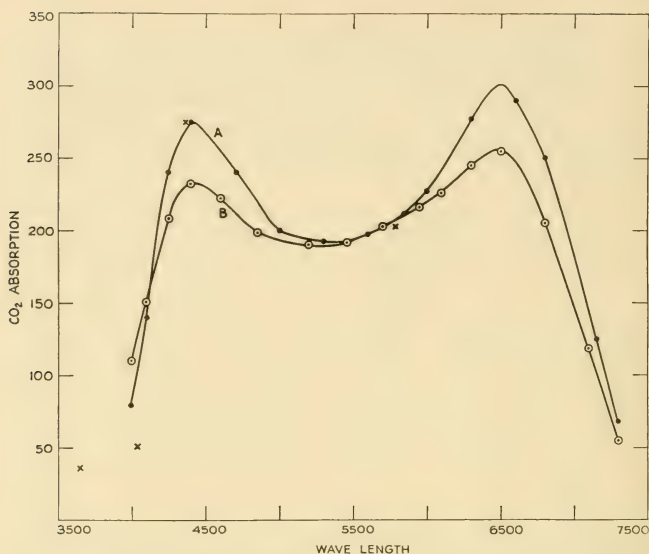


FIG. 3.—Wave-length assimilation curves. A, results obtained with large Christiansen filters and sunlight; B, results obtained with 6-inch Christiansen filters and Mazda lights. Points marked X, the results obtained with the line filters and quartz mercury arc.

TABLE 1.—Carbon Dioxide Absorption in Different Wave-length Regions  
(Original uncorrected mean values)

$\lambda$	Large Christiansen filters	$\lambda$	Small Christiansen filters	$\lambda$	Corning line filters
4000	80	4000	110	3650	37
4100	140	4100	151	4048	52
4250	240	4250	208	4358	275
4400	275	4400	232	5461	193
4700	240	4600	222	5780	203
5000	200	4850	199		
5300	193	5200	191		
5461	193	5461	193		
5600	198	5700	204		
5850	212	5950	217		
6000	227	6100	226		
6300	277	6300	245		
6500	301	6500	255		
6600	295	6800	205		
6800	250	7100	118		
7150	125	7300	55		
7300	68				

## CORRECTION OF CURVES FOR STRAY LIGHT

These curves of photosynthesis and wave length may be regarded as approximately correct, but need improvement because the Christiansen filters, besides the predominant wave lengths, transmitted others in lesser degrees.

Consider, for example, any wave length, as at the blue maximum of curve A in figure 3, connecting photosynthesis and wave length. For brevity call such a wave length  $W_0$ . On either side of this spectral point consider equal wave-length intervals of width  $a$  to be set off. Thus we reach wave lengths  $[W_0 - ma]$ ,  $[W_0 - (m-1)a]$ , . . . .  $[W_0 - a]$ ,  $[W_0]$   $[W_0 + a]$ , . . . . ,  $[W_0 + (n-1)a]$ ,  $[W_0 + na]$ . Consider this succession of equally spaced wave-length places to extend from the wave length  $[W_0 - ma]$ , where the Christiansen filter ceases to transmit shorter waves appreciably, or else where photosynthesis sensibly ceases, to the wave length  $[W_0 + na]$  where it ceases to transmit longer waves appreciably, or else where photosynthesis sensibly ceases.

We have now to deal with two curves: 1, the approximately determined curve of photosynthesis and wave length; 2, the curve of energy transmission and wave length for that Christiansen filter which transmits predominantly the wave length  $W_0$ .

Let  $[e_0]$ ,  $[e_{-m}]$  . . . .  $[e_{-1}]$ ,  $[e_{+1}]$  . . . .  $[e_{+n}]$  represent the ordinates of curve no. 1 at the wave length region  $W_0$  and at wave lengths situated at equal intervals of width  $a$  on either side, thus covering the whole range of spectrum from the place  $[W_0 - ma]$  to  $[W_0 + na]$ . Let  $[C_0]$ ,  $[C_{-m}]$  . . . .  $[C_{-1}]$ ,  $[C_{+1}]$  . . . .  $[C_{+n}]$  be the areas included under the curve no. 2 above described, within intervals of wave length  $a$  from the wave length  $[W_0 - ma]$  to the wave length  $[W_0 + na]$ . These areas will be proportional respectively to the energy transmitted by the Christiansen filter which transmits predominantly the wave length  $W_0$ , but whose transmission extends in sensible degree all the way between wave length  $[W_0 - ma]$  and  $[W_0 + na]$ . The sum total of these areas we may call  $q$ , proportional to the total amount of energy of radiation transmitted by the filter. If we divide the measured areas  $[e_{-m}]$  . . . .  $[e_{+n}]$  by the sum total of these areas, the new values of  $[e_{-m}]$  . . . .  $[e_{+n}]$  will represent the fractional part of the total energy  $q$  in each wave length interval  $a$  from the wave length  $[W_0 - ma]$  to  $[W_0 + na]$ , and  $\Sigma(e_{-m} . . . . . e_{+n}) = 1$ .

Inasmuch as the curve no. 1 described above represents approximately the dependence of photosynthesis on wave length, therefore the products  $[e_{-m}C_{-m}]$  . . . .  $[e_0C_0]$  . . . .  $[e_{+n}C_{+n}]$  will each repre-

sent approximately the amount of photosynthesis contributed by an element of spectrum of width  $a$  which is transmitted by that Christiansen filter which predominantly transmits wave length  $W_0$ . The sum total of these products  $\Sigma(e_{-m}C_{-m} \dots e_0C_0 \dots e_{+n}C_{+n})$  represents the total photosynthesis, originally measured as  $e_0$ . Of this sum of products only one,  $e_0C_0$ , represents the photosynthesis that is produced by radiation lying between the wave lengths  $[W_0 - \frac{1}{2}a]$  and  $[W_0 + \frac{1}{2}a]$ . But this interval contains the fraction  $C_0$  of the total amount of energy of radiation which was employed in the experiment at wave length  $W_0$ .

We find, then, that in the experiment, as actually performed,  $C_0q$  of energy produced

$$e_0 \times \frac{e_0C_0}{\Sigma(e_{-m}C_{-m} \dots e_0C_0 \dots e_{+n}C_{+n})}$$

of photosynthesis. Had the full unit quantity,  $q$ , of radiation of wave length  $W_0$  been used, then the amount of photosynthesis would have been (according to the first approximation):

$$\frac{e_0}{C_0} \times \frac{e_0C_0}{\Sigma(e_{-m}C_{-m} \dots e_0C_0 \dots e_{+n}C_{+n})}$$

Performing a similar operation at all wave lengths where photosynthetic measurements were made, we are now able to plot a new curve in place of curve no. 1, somewhat closer to the true form which the photosynthetic curve should take. This new curve may now be used as a new point of departure to obtain a still better approximation. That is to say, starting a second time with the original curve no. 1, we employ the corrected form of it, not itself, in determining new and better correction factors by which to multiply the ordinates of the original curve no. 1 to obtain from it a still better approximation to the true form desired. It has been found desirable to repeat these steps twice in case of curve A obtained with the large Christiansen filters and three times in case of curve B obtained with the small filters. After that no appreciable change in the form occurred and the process was discontinued.

A numerical example of the first corrected approximation is given in table 2, for wave length above defined as  $W_0$ . In the example  $W_0$  is 4600 A and the wave-length intervals  $a$  are 200 A.

Using the results given in table 2,

$$\frac{e_0}{C_0} \times \frac{e_0C_0}{\Sigma(e_{-m}C_{-m} \dots e_0C_0 \dots e_{+n}C_{+n})} = \frac{257}{.700} \frac{257 \times .700}{249.7} = 265$$

the first approximation of the amount of photosynthesis produced at 4600 A as originally measured was 257.

In table 2, column 1 gives the wave lengths at the center of the wave-length intervals, column 2 the fractional part of the total energy transmitted by the filter in the various wave-length intervals, column 3 the measured values of photosynthesis, and column 4 the approximate amount of photosynthesis contributed by each wave-length interval. The sum total of column 4 represents the amount of photosynthesis originally measured as 257.

A similar operation was performed for each 200 Å wave-length interval for the whole spectral region covered by the photosynthetic measurements. These values represent the first corrected approximation to the photosynthesis and wave length curve. Subsequent corrected approximations will be understood by what has been said in the preceding paragraphs.

In table 3, column A represents the measured values of photosynthesis determined with the large Christiansen filters, and columns A<sub>1</sub>, A<sub>2</sub>, and A<sub>3</sub> are the first, second, and third corrected approximations, respectively. Column B represents the measured values of photosynthesis obtained with the small filters, and columns B<sub>1</sub>, B<sub>2</sub>, B<sub>3</sub>, and B<sub>4</sub> are the first, second, third, and fourth corrected approximations, respectively. Only small changes occur in the form of the curves after the first corrected approximation in case of the large filters, and after the second corrected approximation in case of the small filters.

### FINAL RESULTS

The final corrected results, in each case, have been plotted in figure 4. Curve A<sub>3</sub>, the corrected form of the curve obtained with the large Christiansen filters, is considered to be the curve nearest to the true form of the photosynthesis-wave-length curve.

The points on the original curve are based on the mean of five or more determinations of the ratio between the photosynthesis produced at 5461 Å and at the wave length at the given point. Individual determinations did not vary on the average more than 4 percent from the mean ratio. Thus we may assume that the original values of the photosynthesis produced by the energy transmitted by the various filters are accurate to about  $\frac{4}{\sqrt{4}}$  percent or 2 percent.

In correcting the original curve another source of error is possible. The distribution of energy transmitted by the large Christiansen filters was measured by a double monochromator on clear days, near noon. Since the distribution of energy in sunlight varies with the transparency of the air, it is not certain that the measured values

TABLE 2.—*Data Used in the Calculation of the first Corrected Approximation to the True Value of Photosynthesis at 4600 Å*

$(W_{-m} \dots W_0 \dots$ $\dots W_{+n})$	$(C_{-m} \dots C_0 \dots$ $\dots C_{+n})$	$(e_{-m} \dots e_0 \dots$ $\dots e_{+n})$	$(e_{-m} C_{-m} \dots e_0 C_0 \dots$ $\dots e_{+n} C_{+n})$
4000	0	80	0
4200	.004	211	0.8
4400	.106	275	29.1
4600	.700	257	180.0
4800	.122	225	27.4
5000	.033	200	6.6
5200	.018	193	3.5
5400	.013	193	1.5
5600	.004	198	0.8
5800	0	200	0
Sum.....			249.7

TABLE 3.—*Corrected Values of Carbon Dioxide Absorption in Different Wave-length Regions*

$\lambda$	Large Christiansen filters				Small Christiansen filters				
	$A$	$A_1$	$A_2$	$A_3^*$	$B$	$B_1$	$B_2$	$B_3$	$B_4^*$
4000	80	64	51	50	110	85	65	60	55
4200	211	219	223	223	223	189	196	202	206
4400	275	289	292	292	232	267	275	280	281
4600	257	265	263	263	222	249	251	254	254
4800	225	226	226	227	203	218	218	220	221
5000	200	199	200	200	194	203	199	197	196
5200	193	189	190	190	191	199	193	191	190
5400	193	188	185	186	191	203	194	191	190
5600	198	193	190	191	198	213	203	199	198
5800	208	199	194	194	207	228	219	214	213
6000	227	224	219	218	220	247	236	228	225
6200	260	270	264	264	236	275	268	264	263
6400	295	328	329	330	253	316	321	324	325
6600	295	345	351	352	248	320	330	335	336
6800	250	301	305	307	205	275	277	279	280
7000	177	212	213	214	149	185	190	191	192
7200	105	123	124	124	86	98	100	102	103
7400	30	22	16	13	25	22	16	13	11

\* Final results.

for the various filters represents the real distribution at the time of observation. This factor may account for a large part of the variations in the original observations.

In order to form an estimate of the importance of this source of error for the corrected curve, I computed two sets of energy distribution curves, one for a hazy day and the other for a clear day. Following the method given above, two forms of the corrected curve

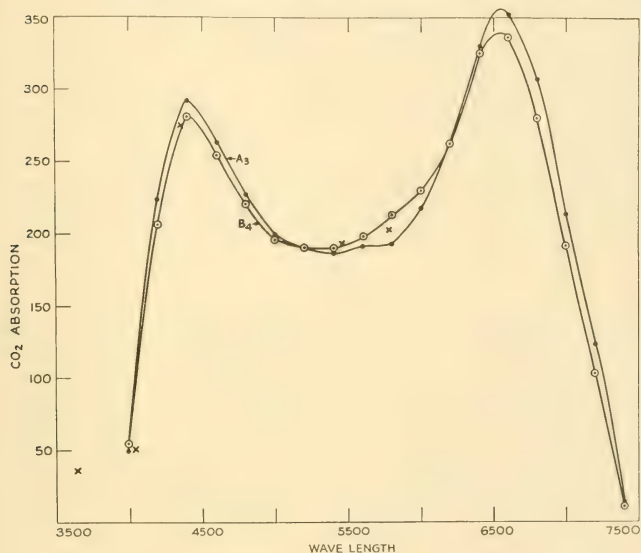


FIG. 4.—Wave-length assimilation curves.  $A_3$ , the corrected form of the curve obtained with the large Christiansen filters;  $B_4$ , the corrected form of the curve obtained with the small Christiansen filters. Points marked X, the results obtained with the line filters and quartz mercury arc.

were obtained. The maximum difference between these curves was about 3 percent. This difference represents two extreme cases; thus we may assume that the corrected curve would not be changed by more than half the error mentioned. This error added to the error of the original measurements would indicate that curve  $A_3$  represents the true form of the photosynthesis-wave-length curve to a probable error of about 4 percent. The curve  $B_4$ , as well as the values obtained with the line filters, agree with curve  $A_3$ . The difference is 5 percent or less except in a short wave-length interval near 5800 Å. Values



for wave lengths longer than 6800 Å are probably in error by more than 5 percent, since they are materially affected by the assumption that photosynthesis ceases at 7500 Å.

Some measurements made by Dr. McAlister, in this laboratory, on the amount of light transmitted by a wheat leaf, combined with data by Shull (1929) on the reflecting power of green leaves, show that less photosynthesis may be expected in the green region, owing to the fact that the leaves transmit and reflect a larger portion of the incident radiation in this region. Although it is not possible as yet to interpret the results of my experiments in terms of equal *absorbed* energy, a correction for the reflecting power and transmission of the leaf would probably raise the photosynthetic activity of absorbed green radiation to be equal to or greater than that for the blue region. There may probably still be a maximum in the red.

The long wave-length limit of photosynthesis appears to be between 7200 Å and 7500 Å. Using the strong line of mercury, some slight amount of photosynthesis was still found at 3650 Å in the ultraviolet.

### SUMMARY

The rate of photosynthesis on the basis of equal incident energy was determined as a function of the wave length of light for a wheat plant. The entire visible spectrum is effective in producing photosynthesis. The wave-length limits, although not accurately determined, appear to be between 7200 Å and 7500 Å on the red end, and less than 3650 Å on the blue end of the spectrum. A principal maximum occurs at 6550 Å in the red, and a secondary one at 4400 Å in the blue. Increased reflection and transmission of radiation in the green region by plant leaves diminish the effectiveness of incident green rays to promote photosynthesis.

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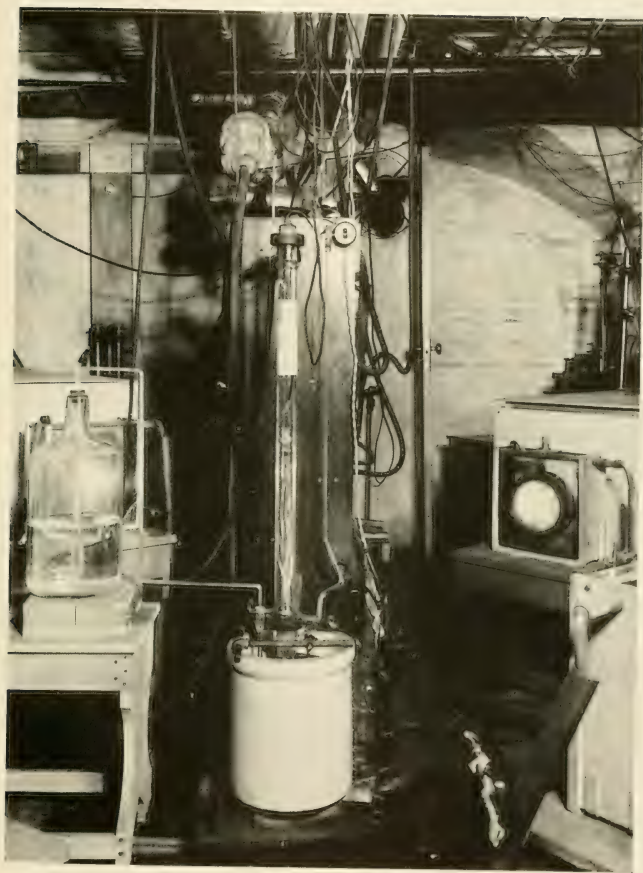
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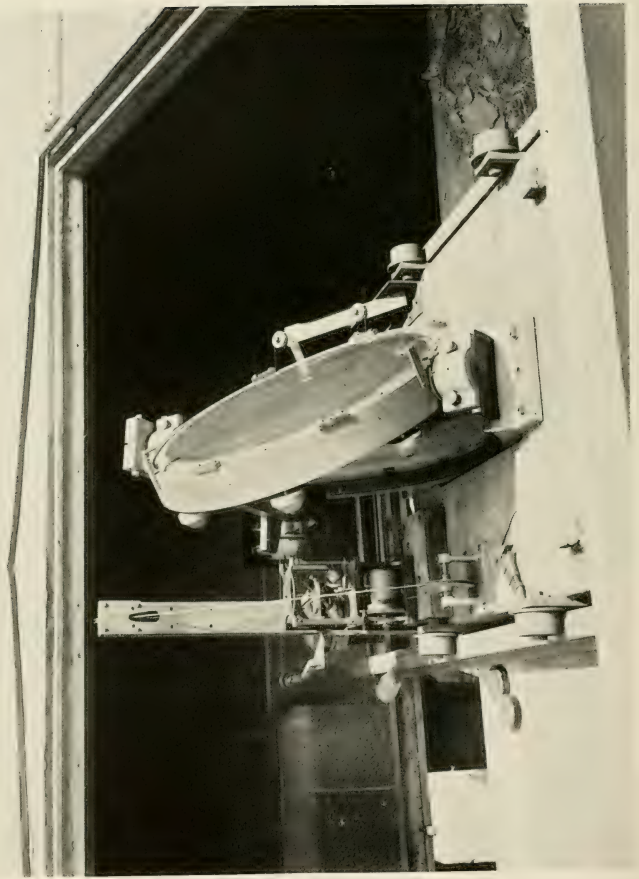
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A GENERAL VIEW OF THE APPARATUS SHOWING THE GROWTH CHAMBER  
AND ONE OF THE 6-INCH CHRISTIANSEN FILTERS



THE 30-INCH MIRROR COELOSTAT



THE 12 BY 14 INCH CHRISTIANSEN FILTER AND TEMPERATURE  
CONTROL SYSTEM

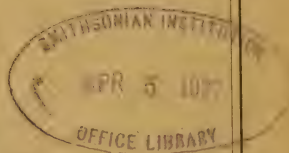




SMITHSONIAN MISCELLANEOUS COLLECTIONS  
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THIRD CONTRIBUTION  
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This is the third paper in a series dealing with nomenclatural changes necessary for Cambrian species.<sup>1</sup> As in the previous papers, only trilobites are included, the nontrilobitic species being reserved for separate printing. Also, the former plan of arrangement in alphabetical order according to genera is continued. As a rule, foreign species from regions where specialists are known to be at work have not been considered.

### ALBERTELLA Walcott, 1908

#### *Albertella cimon* (Walcott)

*Zacanthoides ? cimon* WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 2, p. 41, pl. 7, fig. 6, 1917 (fig. 6a an indeterminate fragment of *Kootenia*).

Middle Cambrian, Ptarmigan; (loc. 63b) Ptarmigan Peak, near Lake Louise, Alberta.

*Holotype*.—U.S.N.M. no. 63767.

### ANTAGMUS Resser, 1936

#### *Antagmus pia* (Walcott)

*Ptychoparia pia* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 93, pl. 12, fig. 8, 1917.

Lower Cambrian, Mount Whyte; (loc. 35f) Mount Stephen, near Field, and (loc. 35h) Mount Bosworth, British Columbia.

*Holotype*.—U.S.N.M. no. 64391.

#### *Antagmus cuneas* (Walcott)

*Ptychoparia cuneas* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 87, pl. 11, fig. 4, 1917.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 64369.

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<sup>1</sup> Resser, Charles Elmer, Nomenclature of some Cambrian trilobites, Smithsonian Misc. Coll., vol. 93, no. 5, Feb. 14, 1935; Second contribution to nomenclature of Cambrian trilobites, idem, vol. 95, no. 4, April 1, 1936.



**Antagmus cleon (Walcott)**

*Ptychoparia cleon* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 84, pl. 12, fig. 10, 1917.

The figured specimen is not fully characteristic of the genus, but an unillustrated, better preserved cranidium in the same lot is more typical.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 64393.

**Antagmus skapta (Walcott)**

*Ptychoparia skapta* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 95, pl. 12, fig. 9, 1917.

Lower Cambrian, Mount Whyte; (loc. 62w) Gog Lake, Wonder Pass, Alberta.

*Holotype*.—U.S.N.M. no. 64392.

**APHELASPIS Resser, 1935****Aphelaspis wyomingensis (Miller)**

*Crepicephalus ? wyomingensis* MILLER, Journ. Pal., vol. 10, no. 1, p. 29, pl. 8, figs. 9-12, 1936.

Upper Cambrian; Crow Creek, 3 miles north of Tipperary, Owl Creek Range, Wyoming.

*Cotypes*.—Columbia Univ. nos. 12601-3.

**ARAPAHOIA Miller, 1936****Arapahoia ransomei (Stoyanow)**

*Hesperaspis ransomei* STOYANOW, Bull. Geol. Soc. Amer., vol. 47, no. 4, p. 468, pl. 1, figs. 6, 7, 1936.

Upper Cambrian, Abrigo; Whetstone Mountains, Arizona.

*Cotypes*.—Presumably Univ. Arizona.

**Arapahoia butleri (Stoyanow)**

*Hesperaspis butleri* STOYANOW, Bull. Geol. Soc. Amer., vol. 47, no. 4, p. 469, pl. 1, fig. 8, 1936.

Occurrence same as preceding.

*Holotype*.—Presumably Univ. Arizona.

**ASAPHISCUS Meek, 1873****Asaphiscus spathus (Mason)**

*Anomocarella ? spatha* MASON, Bull. South California Acad. Sci., vol. 34, pl. 2, p. 107, pl. 15, fig. 10, 1935.

Middle Cambrian, Cadiz; Marble Mountains, California.

*Holotype*.—Los Angeles Mus. no. A 2471-10.

**BERKEIA, n. gen.**

*Diagnosis*.—Small trilobites. Cranidium considerably arched. Glabella over two-thirds length of the cranidium, slightly tapered, rounded in front. Two pairs of glabellar furrows well impressed. Fixigenes convex, less than half the width of glabella. Brim about as wide as the fixigene, consists of convex preglabellar area and a narrower somewhat swollen rim.

Pygidium also convex, with the axis extending to rear margin, and with two well-marked furrows followed by faint ones.

*Genotype*.—*Agraulos convexus* var. *B. Berkey*.

***Berkeia typica*, n. sp.**

*Agraulos convexus* var. *B. BERKEY*, Amer. Geol., vol. 21, p. 288, pl. 20, figs. 5, 6, 1898.

The generic description cites the features of the species.

Upper Cambrian, Ironton; (loc. 82b) Taylors Falls, Minnesota.

*Holotypes*.—Columbia Univ. no. 22285.

**BLOUNTIA Walcott, 1916*****Blountia glabra* (Walcott)**

*Asaphiscus (Blainia) glabra* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 5, p. 394, pl. 63, figs. 1-1e, 1916.

Upper Cambrian, Nolichucky; (loc. 107x) Bull Run Knobs, 11 miles northwest of Knoxville, Tennessee.

*Cotypes*.—U.S.N.M. nos. 62804-6.

**BOLASPIDELLA, n. gen.**

A small trilobite from the Middle Cambrian Wheeler shale fails to fit any existing genus. It is represented by only a few cranidia among the thousands of specimens collected from these beds. At first glance it is like *Bolaspis*, particularly like *B. errata* which has only a slight boss, but cannot be retained in the genus because the preglabellar area is wholly depressed.

*Diagnosis*.—Small trilobites with a roughly quadrangular cranidium. Glabella small, extending about two-thirds the length of the cranidium, arched. Glabellar furrows faint or lacking. Occipital ring heavy, extending into a stout spine. Fixigenes wider than glabella, rising from the dorsal furrow to the eyes. Eyes prominent, somewhat less than median in size. Eye lines rather heavy, straight. Brim rather wide, with a rolled rim and nearly flat preglabellar area.

*Genotype*.—*Ptychoparia housensis* Walcott.

***Bolaspidella housensis* (Walcott)**

*Ptychoparia housensis* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 201, pl. 25, fig. 5, 1886.

Middle Cambrian, Wheeler; (loc. 4) Antelope Spring, House Range, Utah.

*Holotype*.—U.S.N.M. no. 15443.

**BONNIELLA, n. gen.**

Members of the long-ranging trilobite group to which *Bonnia*, *Kootenia*, *Olenoides*, and other genera belong are numerous in Lower and Middle Cambrian rocks. For example, *Bonnia*, wherever present, is usually represented by many species and thousands of individuals. A monographic study of this trilobite group has now gone far enough to warrant a few generalizations. In the first place few of the genera can be determined by cranidia alone, so that genera and even species must be made on pygidia, and the cranidia matched as nearly as possible by association, surface markings, or by proportionate dimensions. In the second place the genera grade one into the other, so that arbitrary lines of separation must be chosen, which for instance between *Bonnia* and *Kootenia* is the degree of fusion of pygidial pleural segments, and between *Kootenia* and *Olenoides*—both with pleural separations visible—is the unequal width of the two portions of the pleuron resulting from the diagonal course of the pleural furrow. A third generalization apparently warranted is that marginal or axial spines have nothing more than a specific value. Within a genus the marginal spines may vary from mere waviness of the margin near the anterior angles to a full suite of spines, sometimes longer than the pygidium. These and other modifications of the fundamental group characteristics tend to come and go with the passage of time.

Another modification not mentioned in the foregoing lines is the development of a flattened marginal extension instead of spines, which rather strangely seems to be accompanied by expansion of the anterior portion of the glabella. This tendency in the Lower Cambrian has given rise to the forms grouped under the new generic name *Bonniella*, and in late Middle Cambrian it has produced *Holteria*.

*Bonniella* is primarily characterized by the pygidial flange back of the second segment. Exclusive of this feature, the pygidium is typical of *Bonnia* in general appearance and in the presence of marginal spines at the anterior angles, but it has less complete pleural fusion than in the majority of species belonging to *Bonnia*. The cranidium, as in *Bonnia* and other members of the family, is quadrate. In

*Bonniella* the glabella is highly arched transversely with a steep anterior slope and has a tendency to expand forward. Two sets of short, reflexed glabellar furrows are generally clearly defined. In the three species now known the cranidium is granulose, but such markings are not observable on the pygidia.

*Genotype*.—*Olenoides (Dorypyge) desiderata* Walcott.

***Bonniella desiderata* (Walcott)**

*Olenoides (Dorypyge) desiderata* WALCOTT, U. S. Geol. Surv. 10th Ann. Rep., p. 644, text fig. 67, 1891.

*Dorypyge desiderata* MATTHEW, Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 187, 1897.

The glabella of this species is strongly granulose and evidently had an occipital spine. The pygidium of *B. desiderata* has broad marginal flanges which extend outward and backward at the posterior angles for a considerable distance. In keeping with this development the two marginal spines at the anterior angles are long and slender.

Lower Cambrian, Winooski; (loc. 26) 1½ miles southeast of Highgate Springs, Vermont.

*Cotypes*.—U.S.N.M. no. 18452.

**BRISCOIA Walcott, 1924**

***Briscoia nevadensis*, n. sp.**

*Dicellosephalus osceola* WALCOTT (not Hall), U. S. Geol. Surv. Mon. 8, p. 40, pl. 9, fig. 25, 1884.

This trilobite was referred to Hall's Wisconsin species of *Osceolia*, but it clearly belongs to *Briscoia*. *B. nevadensis* is smaller than most other species referred to the genus, and at the same time has a narrow glabella and slender pygidial axis.

Upper Cambrian, Hamburg; (loc. 66) north of the Dunderburg mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24659.

**CEDARIA Walcott, 1924**

***Cedaria milleri*, n. sp.**

*Cedaria* cf. *prolifera* MILLER, Journ. Pal., vol. 10, no. 1, p. 28, pl. 8, fig. 18, 1936.

The small Wyoming species has a less advanced direction for the posterior portion of the facial suture, and a narrower preglabellar area than *C. prolifera*.

Upper Cambrian, Du Noir; Warm Springs Creek, 2 miles west of Du Noir, Wind River Range, Wyoming.

*Holotype*.—Columbia Univ. no. 12632.

## CONASPIS Hall, 1863

*Conaspis* HALL, 16th Ann. Rept. New York State Cab. Nat. Hist., p. 152, 1863.

*Conaspis* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357 (footnote), 1914.

*Macrotoxus* LORENZ (part), 1906, Zeitschr. Deutsch. Geol. Gesell., bd. 58, p. 61.

Hall stated, "Should the species possessing these features be found to require separation from *Conocephalites*, I would propose the name *Conaspis*." Thus was the genus *Conaspis* established, and no further study has been given it except the brief diagnosis in the footnote given by Walcott. However, both authors had a group of genera in mind, and hence their diagnoses are quite general.

As pointed out by Walcott, Lorenz referred two species to his genus *Macrotoxus*, one being *Anomocare angelini* Grönwall and the other *Conocephalites perseus* Hall. The latter was stated to be from the Mount Stephen fossil bed in British Columbia, hence it is not clear whether he was considering Hall's Upper Cambrian *C. perseus* and merely made an error in recording the locality or whether a Middle Cambrian trilobite from Canada was in mind. It is possible that Lorenz had knowledge of specimens of *Elrathina cordillerae* that Matthew had identified as *C. perseus*. Furthermore, *Anomocare angelini* does not even belong to the same trilobite family as *C. perseus* and will receive the name *Macrotoxus* if it should prove to be distinct from *Anomocare*; otherwise *Macrotoxus* becomes a synonym of *Anomocare* and not of *Conaspis* as stated by Walcott.

Walcott chose *Conocephalites perseus*, the species first on Hall's list as the genotype. Unfortunately, Hall's figure of *C. perseus* is inaccurately drawn and the type locality is lost owing to the discontinuance of the postoffice then known as Kickapoo, but as Hall's types are in the American Museum of Natural History, no questions as to the generic features remain.

*Diagnosis*.—Cephalon, excluding the posterolateral limbs, roughly rectangular. Eyes situated at about midlength, with the facial suture diverging slightly anterior to them, and intramarginal almost or altogether to the center. Posterior facial suture diverging rapidly, forming triangular posterolateral limbs. Dorsal furrows converge slightly and join across the front of the glabella in a rather straight line. Two or three pairs of glabellar furrows lightly impressed, the rear pair joining in the middle along a horizontal course. Palpebral lobes rather small and strongly bowed. Brim with a width about a third of the length of the cephalon. Rim defined by a sharp but shallow furrow, thickened, tapering laterally because of the intramarginal course of the suture.

*Fixigenes* convex, rather wide, with a rim defined by a shallow furrow. Genal spine sharp, sometimes as long as the cheek is wide, and is directed straight out in line with the margin.

Thoracic segments appear to have a strong furrow and considerable backward bend at the fulcrum. Tips sharp and long.

Pygidium short and transverse, tending to be triangular in outline. Axis elevated above rather flat pleural lobes. Three or more axial rings are well defined. Pleura fused, in some species sufficiently to eliminate the separating furrows. Most or possibly all species carry delicate marginal spines but in some species only the anterior segment is thus developed. Rear margin sometimes indented medianly.

*Gnotype*.—*Conocephalites perseus* Hall.

#### **Conaspis perseus (Hall)**

*Conocephalites perseus* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 153, pl. 7, figs. 17-23; pl. 8, fig. 33, 1863.

*Conaspis perseus* HALL, idem, p. 152; WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357 (footnote), 1914.

Upper Cambrian, Franconia; opposite the mouth of the Chippewa River, Minnesota. Kickapoo and many other localities, Wisconsin.

*Cotypes*.—A.M.N.H. no. 319.

#### **COOSIA Walcott, 1913**

##### **Coosia onusta (Whitfield)**

*Crepicephalus onustus* WHITFIELD, Ann. Rep. Wisconsin Geol. Surv., p. 53, 1878; Geol. Wisconsin, vol. 4, p. 182, pl. 1, figs. 22, 23, 1882.

*Anomocarella onusta* WALCOTT, Smithsonian Misc. Coll., vol. 64, no. 3, p. 204, 1916.

Upper Cambrian, Eau Claire (Cedaria zone); Eau Claire and other localities in Wisconsin.

*Holotype*.—Univ. Wisconsin.

##### **Coosia connata (Walcott)**

*Ptychoparia connata* WALCOTT, Proc. U. S. Nat. Mus., vol. 13, p. 272, pl. 21, fig. 2, 1890.

Upper Cambrian, Eau Claire (Crepicephalus zone); (loc. 78a) Eau Claire and other localities in Wisconsin.

*Holotype*.—U.S.N.M. no. 23855.

##### **Coosia wyomingensis, n. sp.**

*Bathyriscus* sp., WALCOTT, U. S. Geol. Surv. Mon. 32, p. 466, pl. 64, fig. 6, 1899.

The pygidium on which this species is based is rather blunt, but fully typical of the genus. Most of the surface is exfoliated and there-



fore shows pleural grooves and furrows much more strongly than on the exterior.

Upper Cambrian; Dead Indian Creek, Clark Fork, Wyoming.

*Holotype*.—U.S.N.M. no. 94343.

#### DAWSONIA Hartt, 1868

*Dawsonia* HARTT, in Dawson, *Acadian Geol.*, 2d ed., p. 655, 1868.

*Goniodiscus* RAYMOND, *Ottawa Nat.*, vol. 27, p. 101, 1913.

*Calodiscus* HOWELL, *Journ. Pal.*, vol. 9, no. 3, 224, 1935.

In the second edition of "Acadian Geology" published in 1868, Dawson, p. 641, quotes Hartt's preliminary report on the first Cambrian fossils discovered in maritime Canada, which appeared in Bailey's "Observations on the Geology of New Brunswick", 1865. On page 643 Dawson makes the following statement: "other engagements have prevented Mr. Hartt from fulfilling his intention of publishing detailed descriptions of the species. In compliance, however, with my desire to place these interesting forms before geologists in this work, he has kindly communicated to me his ms. notes; and I have extracted from these the following descriptions of several of the more common species." Then follows descriptions of 26 species, of which 12 are illustrated.

A figure and description of *Microdiscus dawsoni* appears on page 654. The first paragraph on the following page is written in the first person, but it is not clear whether it was Dawson writing or whether he was merely quoting Hartt. However, a note is appended by Dawson in the second paragraph which reads as follows: "Mr. Hartt had originally described this species under the new generic name of *Dawsonia*; but Mr. Billings regards it as a species of *Microdiscus* of Salter." From this statement it is evident that Hartt described this trilobite as *Dawsonia dawsoni* and that Dawson, without Hartt's direction referred the species to the invalid genus *Microdiscus* Emmons (not Salter). Consideration of these facts warrants the conclusion that *Dawsonia* is a valid genus for this and its related species. Subsequently, *Dawsonia* was used several times—by Carpenter and by Nicholson in 1873 and by Fritsch by 1879—but this does not invalidate its application to a trilobite by Hartt in 1868.

In 1913 Raymond reviewed this group of trilobites, proposing *Goniodiscus* for the species of *Dawsonia*. His argument that *Dawsonia* could not be restored because meanwhile it had been applied to another animal, is, of course, not well founded, for even if *Dawsonia* had been synonymous with *Microdiscus* when proposed in 1868 its further use in 1873 would not have been allowable.

Inasmuch as *Goniodiscus* proposed by Raymond in 1913 was previously used in 1842, Howell substituted *Calodiscus*.

Therefore, when the history of these generic names is reviewed *Dawsonia* appears to have been clearly established and subsequent changes were unnecessary.

Besides the genotype the following species seem to belong to *Dawsonia*:

- Goniodiscus lobata* (Hall)
- Calodiscus oclandicus* Westergaard
- Goniodiscus parkeri* (Walcott)
- Microdiscus sculptus* Hicks
- Calodiscus foveolatus* Howell

The family name would, according to the rules, become Dawsonidae, which would contain the genera *Dawsonia* Hartt, *Eodiscus* Matthew and *Weymouthia* Raymond.

*Genotype*.—*Dawsonia dawsoni* Hartt = *Microdiscus dawsoni* Billings.

#### DUNDERBERGIA Walcott, 1924

##### *Dunderbergia anyta* (Hall and Whitfield)

*Crepicephalus* (*Loganellus*) *anytus* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 219, pl. 2, figs. 19-21, 1877.

*Liostracus anytus* BRÖGGER, Geol. Fören. Stockholm Förhandl., vol. 8, p. 212, 1886.

This form is not quite typical of the genus because it is narrow. Also, the surface is more heavily lined than usual.

Upper Cambrian, Secret Canyon; Schellbourne, Schellbourne Range, Nevada.

*Lectotype and paratype*.—U.S.N.M. no. 24576.

#### EHMANIA Resser, 1935

##### *Ehmania tetonensis* (Miller)

*Marjumi* ? *tetonensis* MILLER (part), Journ. Pal., vol. 10, no. 1, p. 33, pl. 8, figs. 19, 20, 1936 (not fig. 21 = *Kootenia tetonensis*).

Middle Cambrian, Wolsey; South Fork, Teton Creek Canyon, Teton Range, Wyoming.

*Cotypes*.—Columbia Univ. no. 12607.

##### *Ehmania adina* (Walcott)

*Ptychoparia adina* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 78, pl. 12, figs. 3-3b, 1917.

Middle Cambrian, Stephen?; (loc. 57q) Mount Bosworth, British Columbia.

*Cotypes*.—U.S.N.M. nos. 64383-5.

**EHMANIELLA, n. gen.**

It seems necessary to make a genus for the forms which are about midway between *Ehmania* and *Elrathia*.

Compared to *Ehmania*, *Ehmaniella* is characterized by the greater width of the cranidium, heavier eye lines, vertical striae on the wider preglabellar area, and a pygidium with fewer segments. The glabella and fixigenae are apt to be granulose or lined. Comparing the new genus with *Elrathia*, the differences in the cranidium are only minor, except for greater width, but the pygidium of *Ehmaniella* is smaller and has the pleural divisions and furrows more clearly developed, extending to the margin with but little loss.

*Genotype*.—*Crephicephalus* (*Loganellus*) *quadrans* Hall and Whitfield.

***Ehmaniella quadrans* (Hall and Whitfield)**

*Crephicephalus* ? (*Loganellus*) *quadrans* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 238, pl. 2, figs. 11-13, 1877.

*Ptychoparia quadrans* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 199, pl. 29, figs. 4-4b, 1886.

Middle Cambrian, Ophir; north of Brigham, Wasatch Range, and (loc. 31d) Blacksmith Fork Canyon, Bear River Range, Utah.

*Holotype and paratype*.—U.S.N.M. no. 15432.

**ELRATHIA Walcott, 1924*****Elrathia occidentalis* (Walcott)**

*Ptychoparia occidentalis* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 51, pl. 10, fig. 5, 1884.

Middle Cambrian, Eldorado; (loc. 55a) east slope Prospect Mountain, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24612.

***Elrathia palliseri* (Walcott)**

*Ptychoparia palliseri* WALCOTT, Canadian Alpine Journ., vol. 1, pt. 2, p. 244, pl. 3, fig. 6, 1908.

Middle Cambrian, Stephen; (loc. 14s) Mount Stephen, above Field, British Columbia.

*Holotype*.—U.S.N.M. no. 94344.

***Elrathia permulta* (Walcott)**

*Ptychoparia permulta* WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 4, p. 145, pl. 21, fig. 1, 1918 (fig. 2 = *E. dubia*).

Middle Cambrian, Burgess; (loc. 35k) Burgess, near Field, British Columbia.

*Holotype*.—U.S.N.M. no. 65516.

**Elrathia dubia, n. sp.**

*Ptychoparia permulta* WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 4, p. 145, pl. 21, fig. 2, 1918.

This specimen departs in several respects from the typical forms of the genus, even though some features relate it to *E. permulta*. The new species lacks eye lines and is narrower between the eyes. The surface is granulated instead of being striated, and the granules behind the eye-line position both on the glabella and the fixigenes are heavier than they are anterior to that position.

Undescribed species have combinations of the surface markings of *E. permulta* and *E. dubia*, which is a strong reason for retaining the latter in the genus.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 65517.

**ELRATHINA, n. gen.**

A group of species considerably like *Elrathia* at first glance presents uniformly different characteristics, so that another genus must be recognized. In general the trilobites of both groups are similar, particularly in appearance. *Elrathina* has a smaller pygidium which further differs in structure. No great difference is apparent in the cranidium, except the narrower preglabellar area. The thorax, owing to more numerous segments and the necessity of tapering to a smaller tail, becomes more triangular in shape and therefore looks somewhat different.

*Genotype*.—*Conocephalites cordillerae* Rominger.

**Elrathina cordillerae (Rominger)**

*Conocephalites cordillerae* ROMINGER, Proc. Acad. Nat. Sci. Philadelphia, p. 17, pl. 1, fig. 7, 1887.

*Ptychoparia cordillerae* WALCOTT, Amer. Journ. Sci., 3d ser., vol. 36, p. 165, 1888; Smithsonian Misc. Coll., vol. 67, no. 4, p. 144, pl. 21, figs. 4 (3 and 5?), 1918.

Middle Cambrian, Stephen; (loc. 145) Mount Stephen, above Field, British Columbia.

*Holotype*.—Acad. Nat. Sci. Philadelphia; cast, U.S.N.M. no. 17831; plesiotypes, nos. 65518, 57658.

**ELVINIA Walcott, 1924****Elvinia unisulcata (Hall and Whitfield)**

*Crepeicephalus (Loganellus) unisulcatus* HALL and WHITFIELD, U. S. Geol. Expl. Par., vol. 4, p. 216, pl. 2, figs. 22, 23, 1877.

*Ptychoparia unisulcatus* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 58, 1884.

Upper Cambrian, Secret Canyon; (loc. 61) south of the Hamburg Mine, Eureka District, Nevada.

*Cotypes*.—U.S.N.M. no. 24574.

***Elvinia tetonensis*, n. sp.**

*Elvinia roemeri* MILLER, Journ. Pal., vol. 10, no. 1, p. 30, pl. 8, fig. 36, 1936.

Compared with *E. roemeri*, this species has a much shorter brim, which gives the whole cranidium a wider appearance.

Upper Cambrian, Dry Creek; South Fork Teton Canyon Creek, Teton Range, Wyoming.

*Holotype*.—Columbia Univ. no. 12631.

**GLAPHYRASPIS, n. gen.**

*Diagnosis*.—Small trilobite. Glabella rather large, nearly rectangular in outline, well defined by dorsal furrow. Four pairs of short, faint, glabellar furrows. Occipital furrow shallow. Short median, longitudinal furrow in front of glabella. Fixigenes arched, tapering in width from brim to posterior margin. Brim turned downward; rim half or less than half the width of the preglabellar area; anterior furrow shallow. Eyes small, situated well forward. Delicate eye lines have a horizontal direction.

*Name*.—*γλαφυρος* = neat; *ασπίς* = shield.

*Genotype*.—*Liostracus parvus* Walcott.

***Glaphyraspis parva* (Walcott)**

*Liostracus parvus* WALCOTT, U. S. Geol. Surv. Mon. 32, pt. 2, p. 463, pl. 65, fig. 6, 1899.

Upper Cambrian, Dry Creek; (loc. 151f) southeast of Pebble Creek, Yellowstone National Park, Wyoming.

*Holotype*.—U.S.N.M. no. 35233.

**GLYPHASPIS Resser, 1935**

***Glyphaspis nevadensis*, n. sp.**

*Ptychoparia piochensis* WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 201, pl. 26, fig. 2 (only), 1886.

*Ptychoparia kempfi* PACK, Journ. Geol., vol. 14, p. 298, pl. 3, fig. 1, 1906.

As stated in 1935, this cranidium clearly belongs to *Glyphaspis*. If Pack's figure in this instance should be more correctly drawn than his other figures, its reference to this species would be untenable.

Middle Cambrian, Chisholm; (loc. 31) southwest slope of the Highland Range, 3 miles northwest of Pioche and Half Moon Mine, Pioche, Nevada.

*Holotype*.—U.S.N.M. no. 94346.

**Glyphaspis tetonensis, n. sp.**

*Glyphaspis cf. perconcava* MILLER, Journ. Pal., vol. 10, no. 1, p. 30, pl. 8, fig. 17, 1936.

*G. perconcava* Poulsen probably does not belong to the genus, but the Wyoming form does. Compared with the genotype, *G. capella*, the new species has a relatively wider and longer axis, and the pleural grooves run closer to the margin.

Middle Cambrian; South Fork, Teton Canyon Creek, Teton Range, Wyoming.

*Holotype*.—Columbia Univ. no. 12609.

**HAMPTONELLA, n. gen.**

*Diagnosis*.—Minute trilobite. Cranidium nearly quadrate. Glabella unfurrowed, long, rectangular, and narrow. Brim confined to a rim. Fixed cheeks rather wide. Eyes small, situated about the middle of the head.

*Genotype*.—*Ptychoparia fitchi* Walcott.

**Hamptonella fitchi (Walcott)**

*Ptychoparia ? fitchi* WALCOTT, Amer. Journ. Sci., vol. 34, p. 197, pl. 1, fig. 6, 1887; 10th Ann. Rep. U. S. Geol. Surv., p. 650, pl. 96, fig. 5, 1891.

Lower Cambrian, Schodack; (loc. 34) 2½ miles south of North Granville, New York.

*Holotype*.—U.S.N.M. no. 17455.

**HEBEDISCUS Whitehouse, 1936****Hebediscus cobboldi, n. sp.**

*Ptychoparia ? attleboroensis* COBBOLD, Quart. Journ. Geol. Soc. London, vol. 66, p. 23, pl. 3, figs. 11-13, 1910.

*Microdiscus helena* COBBOLD (part), idem, pl. 3, figs. 15, 16, 1910; idem, vol. 67, p. 298, 1911; idem, vol. 76, p. 370, 1921.

*Pagetia ? attleboroensis* COBBOLD, idem, vol. 87, p. 462, pl. 38, figs. 1-5, 6?, 1931.

It appears that the English specimens referred to the Massachusetts species *H. attleboroensis* (Shaler and Foerste) are a distinct species. Evidently those from Newfoundland can be left with *H. attleboroensis*, at least for the present.

*H. cobboldi* differs in having a narrower glabella with somewhat better defined furrows, and the declivity forward of the eye line and glabella is less abrupt.

Lower Cambrian, Olenellus limestone; Comley, Shropshire, England.

*Cotypes*.—Sedgwick Mus. no. A 8.



## IDAHOIA Walcott, 1924

*Idahoia explanata* (Whitfield)

*Conocephalites* (*Ptychaspis*) *explanatus* WHITFIELD, Ann. Rep. for 1879, Wisconsin Geol. Surv., p. 49, 1880; Geol. Wisconsin, vol. 4, p. 181, pl. 1, figs. 27, 28, 1882.

*Ptychoparia explanata* MILLER, N. A. Geol. Pal., p. 565, 1889.

The specimens in the Museum collections identified by Whitfield are used for this generic reference.

Upper Cambrian, Franconia; (loc. 79) Hudson, Wisconsin.

*Holotype*.—Univ. Wisconsin; metatypes, U.S.N.M. no. 94372.

*Idahoia wyomingensis*, n. sp.

*Ptychoparia* (*Lonchocephalus*) *wisconsinensis* WALCOTT (part), U. S. Geol. Surv. Mon. 32, p. 461, pl. 64, figs. 1, 1a, 1899 (not 1b = *I. hamula*; 1c = an undetermined species from Wisconsin).

Walcott's illustrations represent three species, the cranium and cheek from Soda Butte Creek, constituting the new species. The figure copied from Hall is not *I. wisconsinensis* as stated, but *I. hamula*, and the pygidium belongs to an undescribed species, possibly a *Ptychaspis*.

Compared with *I. wisconsinensis*, the new species is somewhat shorter and smaller in size.

Upper Cambrian, Dry Creek; (loc. 151e) Soda Butte Creek, Yellowstone National Park, Wyoming.

*Cotypes*.—U.S.N.M. no. 35225.

## IDDINGSIA Walcott, 1924

*Iddingsia affinis* (Walcott)

*Ptychoparia* (*Euloma*?) *affinis* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 54, pl. 10, fig. 12, 1884; idem, 32, pt. 2, p. 457, pl. 65, fig. 8, 1899.

*Euloma affinis* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 362, 1914.

Upper Cambrian, Secret Canyon; (loc. 63) northeast of Adams Hill, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24642.

## INGLEFIELDIA Poulsen, 1927

*Inglefieldia perola* (Walcott)

*Ptychoparia perola* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 91, pl. 12, fig. 7, 1917.

Although the suture anterior to the eye is less divergent than in species previously assigned to *Inglefieldia*, yet there is no essential difference, and therefore *I. perola* adds a western representative to the genus.

Lower Cambrian, Mount Whyte; (loc. 35m) 3 miles southwest of Lake Louise, Alberta.

*Cotypes*.—U.S.N.M. nos. 64389, 64390.

**KOCHASPIS** Resser, 1935

**Kochaspis kobayashi**, new name

*Chancia* ? *clusia* KOBAYASHI (not Walcott), Journ. Pal., vol. 10, no. 3, p. 165, pl. 21, figs. 25-27, 1936.

Lower Cambrian; Carcajou River, lat. 65° N., northern Mackenzie River, Canada.

*Cotypes*.—Nat. Mus. Canada no. 8713.

**KOOTENIA** Walcott, 1908

**Kootenia tetonensis** (Miller)

*Marjuria* ? *tetonensis* MILLER (part), Journ. Pal., vol. 10, pt. 1, p. 33, pl. 8, fig. 21, 1936 (not figs. 19, 20 = *Ehmania tetonensis*).

Middle Cambrian, Wolsey; South Fork, Teton Creek Canyon, Teton Range, Wyoming.

*Holotype*.—Columbia Univ. no. 12610.

**Kootenia eurekensis**, n. sp.

*Dicellosephalus* ? *quadriceps* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 45, pl. 9, fig. 24, 1884.

Compared with *K. quadriceps* this species is much shorter. It does not have a median eye as shown by Walcott.

Middle Cambrian, Eldorado; (loc. 55b) west side of Secret Canyon, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 15449.

**Kootenia resseri** (Poulsen)

*Dorypyge resseri* POULSEN, Meddels. Grønland, vol. 70, p. 267, pl. 16, figs. 33-35, 1927.

Middle Cambrian, Cape Wood; Cape Kent, North Greenland.

*Cotypes*.—Min. Mus. Copenhagen.

**Kootenia obliquespina** (Poulsen)

*Dorypyge obliquespina* POULSEN, Meddels. Grønland, vol. 70, p. 271, pl. 16, figs. 40-42, 1927.

Middle Cambrian, Cape Wood; Cape Frederick VIII, North Greenland.

*Cotypes*.—Min. Mus. Copenhagen.

**Kootenia serrata (Meek)**

*Bathyrurus serratus* MEEK, 6th Ann. Rep. U. S. Geol. Surv. Terr., p. 480, 1873.

Middle Cambrian, Meagher; northeast of Logan, Montana.

*Holotype and paratypes*.—U.S.N.M. no. 7865.

**Kootenia quadriceps (Hall and Whitfield)**

*Dikellocephalus quadriceps* HALL and WHITFIELD, U. S. Geol. Expl. 40th Par., vol. 4, p. 240, pl. 1, figs. 37-40, 1877.

*Olenoides quadriceps* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 187, pl. 29, figs. 1-1c, 1886.

Middle Cambrian, Ute; Ute Peak, Bear River Range, Utah.

*Cotypes*.—U.S.N.M. no. 15448.

**Kootenia fordii (Walcott)**

*Olenoides fordii* WALCOTT Amer. Journ. Sci., 3d ser., vol. 34, p. 195, pl. 1, figs. 5, 5a, 1887; 10th Ann. Rep. U. S. Geol. Surv., p. 641, pl. 94, figs. 3, 3a, 1891.

*Dorypyge fordii* MATTHEW, Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 187, 1897.

Lower Cambrian, Schodack; (loc. 38c) 1 mile north, and (loc. 38a) 2 miles south of North Granville, New York.

*Cotypes*.—U.S.N.M. no. 17450.

**Kootenia marcoui (Whitfield)**

*Dikellocephalus ? marcoui* WHITFIELD, Bull. Amer. Mus. Nat. Hist., vol. 1, p. 150, pl. 14, fig. 7, 1884.

*Olenoides marcoui* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 186, pl. 26, figs. 5-5b, 1886.

*Dorypyge marcoui* MATTHEW, Trans. Roy. Soc. Canada, 2d ser., vol. 3, sec. 4, p. 187, 1897.

Lower Cambrian, Parker; (loc. 25) Parkers Quarry, Georgia, Vermont.

*Cotypes*.—U.S.N.M. no. 15446.

**Kootenia nana (Ford)**

*Solenopleura nana* FORD, Amer. Journ. Sci., 3d ser., vol. 15, p. 126, 1878.

*Solenopleura nana* WALCOTT, U. S. Geol. Surv. Bull. 30, p. 214, pl. 27, fig. 3, 1886.

*Solenopleura nana* WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 658, pl. 98, figs. 1, 1c-e, 1891.

*Ptychoparia trilineata* WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 203, pl. 27, figs. 1a, 1b, 1886.

Ford did not figure the species when it was described. Since his specimen is not available, the best procedure will be to choose Walcott's earliest figure as the lectotype, which is the one cited in Bulletin 30.

Unfortunately, the lectotype is an imperfect specimen, for which reason reference of the specimens subsequently described from Washington County to the species must remain somewhat doubtful. The pygidia illustrated in 1891 show two species, but whether the difference is merely one of drawing cannot now be determined, since one specimen cannot be found.

Lower Cambrian, Schodack; (loc. 27) Troy, and (loc. 38c) 1 mile north of Middle Granville, New York.

*Lectotype and plesiotypes*.—U.S.N.M. nos. 15425, 17451.

**Kootenia troyensis, n. sp.**

*Solenopleura ? nana* WALCOTT (part), 10th Ann. Rep. U. S. Geol. Surv., p. 658, pl. 98, figs. 1a, 2, 1891 (see *K. nana*).

The illustrations, poor as they are, show the specific difference of this species in size, contour, and width. It may have scattered granules on the test.

Occurrence same as preceding.

*Holotype*.—U.S.N.M. no. 94342.

**Kootenia masoni, new name**

*Dorypyge quadriceps* MASON (not Hall and Whitfield), Bull. Southern California Acad. Sci., vol. 34, pt. 2, p. 116, pl. 15, figs. 18, 20-22, 1935.

This species differs considerably from *K. quadriceps*. The head is shorter, and the pygidium is more completely fused. It is the shortness of the pygidial spines which serves to separate *K. masoni* most easily.

Middle Cambrian, Cadiz; Marble Mountains, California.

*Cotypes*.—Los Angeles Mus., nos. A-2471-18 to 22.

**LITOCEPHALUS, n. gen.**

*Diagnosis*.—Cranidium quadrate or rectangular in outline. Glabella clearly defined, tapered, and truncated in front. Glabellar furrows absent, or a rear pair very faintly indicated. Suture moderately divergent anterior to the eyes. Brim wide. Rim clearly marked, flat but slightly swollen, and more or less upturned. Preglabellar area convex, wide, more than twice width of rim. Eyes of moderate size situated about the middle of the glabella. Fixigenae two-thirds the width of the glabella at the palpebral lobe. Eye lines of moderate development. Test mainly smooth but with other parts unknown.

*Litocephalus* is similar to *Wilbernia*, only two essential differences being apparent. In the first place, *Litocephalus* is much wider, but too few of the species on hand have been studied to ascertain whether this is a generic difference or only merely the results of comparing two

divergent species. The second, unquestionably a valid generic difference, is the manner in which the brim is divided. In *Wilbernia* the rim usually occupies fully two-thirds of the brim, whereas in *Litocephalus* it is always less than half the brim width. *Litocephalus* has vertical striations across the preglabellar area and the anterior outline is straighter.

*Genotype*.—*Dicellosephalus richmondensis* Walcott.

*Name*.— *λίτος* = simple ; *κεφαλος* = head.

***Litocephalus richmondensis* (Walcott)**

*Dicellosephalus richmondensis* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 441, pl. 10, fig. 7, 1884.

*Ptychoparia richmondensis* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 352, 1914.

Upper Cambrian, Secret Canyon ; (loc. 60) opposite the Richmond mine, and (loc. 61) south of the Hamburg Mine, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24616.

***Litocephalus walcotti*, n. sp.**

*Ptychoparia anytus* WALCOTT (not Hall and Whitfield), U. S. Geol. Surv. Mon. 8, p. 56, pl. 9, fig. 26, 1884.

Walcott identified a small cranidium with Hall and Whitfield's species, but besides its smaller size it has a narrower preglabellar area. Its features seem to require its reference to *Litocephalus*. Compared with *L. richmondensis* it has narrower fixigenes.

Upper Cambrian, Secret Canyon ; (loc. 63) northeast of Adams Hill, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24656.

**LONCHOCEPHALUS Owen, 1852**

***Lonchocephalus tipperaryensis* (Miller)**

*Marjunia ? tipperaryensis* MILLER, Journ. Pal., vol. 10, no. 1, p. 33, pl. 8, figs. 15, 16, 1936.

Upper Cambrian ; Crow Creek canyon, 3 miles north of Tipperary, Owl Creek Range, Wyoming.

*Holotype*.—Columbia Univ. no. 12606.

***Lonchocephalus winona* (Hall)**

*Conocephalites winona* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 161, pl. 7, figs. 26-28, 1863.

*Anomocarella ? winona* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 358, 1914.

Upper Cambrian, Eau Claire ; opposite mouth of Black River, and (loc. 84) Dresbach, Minnesota.

*Cotypes*.—A.M.N.H.

**METISIA, n. gen.**

Many heads and tails and several cheeks were recovered from a small limestone boulder at Metis, Quebec. All belong to a single species, which resembles forms younger than Lower Cambrian. Some doubt regarding age remains in all such cases where a fauna is lacking to verify the horizon to which the boulder originally belonged.

*Diagnosis*.—Cranidium simple, highly arched. Glabella large, occupying fully half of the cranidium; dorsal furrow strong; glabella tapered, rounded in front. Glabellar furrows faintly indicated. Occipital furrow deep; neck ring only slightly swollen in the middle. Fixigenes narrow, arched transversely. No eye lines. Eye lobes moderate in size. Brim confined to a swollen rim. Anterior and dorsal furrows join. Facial suture slightly divergent anterior to the eyes; intramarginal for some distance. Anterior angles turned down for a considerable distance.

Libragenes of normal shape and convexity. Rim heavy, widening somewhat at the genal angle. Length of genal spine unknown.

Pygidium with a high, long, and wide axis. About three segments shown in axis and on pleural lobes. Pleura well fused; three pleural furrows clearly defined.

Surface granulose.

*Genotype*.—*Ptychoparia metisensis* Walcott.

***Metisia metisensis* (Walcott)**

*Ptychoparia metisensis* WALCOTT, 10th Ann. Rep. U. S. Geol. Surv., p. 651, text figs. 68a-d, 1891.

Lower Cambrian, boulder in conglomerate; Metis, Quebec.

*Cotypes*.—U.S.N.M. no. 23838.

**MONOCHEILUS, n. gen.**

*Diagnosis*.—Small trilobites with large glabella. Glabella occupies most of head, rounded in front, without glabellar furrows. Brim consists of a single flat, tongue-shaped projection, only as wide as the glabella. Fixigenes lacking. Eyes large; the palpebral lobe arising directly from the dorsal furrow. Posterolateral limbs narrow.

This genus is similar to *Bayfieldia* Clark differing in the lack of fixigenes and in its much larger eyes.

*Genotype*.—*Conocephalites anatinus* Hall.

*Name*.—μονας = single; χελος = brim.



***Monocheilus anatinus* (Hall)**

*Conocephalites anatinus* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 158, pl. 7, figs. 34, 35, 1863.

*Conaspis anatina* Hall, idem, p. 152.

*Conaspis anatina* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357, 1914.

Upper Cambrian, Franconia; Trempealeau, and other localities in Wisconsin.

*Holotype*.—A.M.N.H. no. 329; cast, U.S.N.M. no. 89931.

***Monocheilus micros* (Walter)**

*Conaspis micro* WALTER, Iowa Geol. Surv., vol. 31, p. 185, pl. 11, figs. 5, 6; pl. 12, fig. 2, 1926.

Upper Cambrian, Franconia;  $\frac{1}{2}$  mile southeast of Lansing, Iowa.

*Holotype*.—Univ. Iowa no. 9239.

**ONCHOCEPHALUS, n. gen.**

A group of trilobite species lies between the genera *Inglefieldia* and *Proliostracus* on the one hand, while on the other hand there are features like *Poulsemia*, *Antagmus*. Considered in another sense these forms are about midway between *Syspacephalus* and another new genus being described in a paper on the southern Appalachians. For a long time the question was repeatedly considered from all angles, and finally the conclusion was reached that matters would be simplified if another genus were added. In order to stress the features separating the new genus from those mentioned above, the name *Onchocephalus* was chosen to center attention on the development of the brim.

*Diagnosis*.—Small trilobites in which the cranidium is usually longer than wide. Glabella rather wide, slightly tapered, truncated in front. Glabellar furrows faintly shown to the anterior end of glabella. Contrary to the usual structure in this genus, the anterior pair is more deeply impressed than the others. Fixigenes of nearly even width throughout. Brim of variable width, but always well developed. Pre-glabellar area convex, but variable in width; rim heavy, sometimes greatly expanded, particularly in the center. Eyes small, situated somewhat behind the midpoint of the glabella. Eye lines present.

*Genotype*.—*Ptychoparia thia* Walcott.

*Name*.—*ογκος* = protuberance; *κεφαλος* = head.

***Onchocephalus thia* (Walcott)**

*Ptychoparia thia* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 96, pl. 12, fig. 6, 1917.

Lower Cambrian, Mount Whyte; (loc. 35h) Mount Bosworth, and other localities, British Columbia.

*Holotype*.—U.S.N.M. no. 64388.

***Onchocephalus walcotti*, n. sp.**

*Crepicephalus angusta* WALCOTT (part), U. S. Geol. Surv. Bull. 30, p. 208, pl. 28, fig. 2b (only), 1886; 10th Ann. Rep. U. S. Geol. Surv., p. 653, pl. 96, fig. 9 (only), 1891; Smithsonian Misc. Coll., vol. 64, no. 3, pl. 29, fig. 6 (only), 1916 (other figures represent species of *Kochaspis*).

This species is much like *O. thia*, differing in having a wider brim, which makes the whole cranium relatively longer.

Lower Cambrian, Pioche; (loc. 30) 8 miles north of Bennetts Spring, Highland Range, Utah.

*Holotype*.—U.S.N.M. no. 61642.

***Onchocephalus parvus* (Walcott)**

*Anomocare* ? *parvum* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 59, pl. 9, fig. 17, 1884; U. S. Geol. Surv. Bull. 30, p. 209, pl. 25, fig. 1, 1886; 10th Ann. Rep. U. S. Geol. Surv., p. 653, pl. 96, fig. 2, 1891.

Lower Cambrian, Pioche; (loc. 51) Prospect Mountain, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 15426.

**ORYGMASPIIS, n. gen.**

*Diagnosis*.—Cranidium long and narrow, rather flat in both directions. Glabella over two-thirds the length of the head; slightly tapered and rounded in front; dorsal furrow shallow. Three pairs of glabellar furrows, shallow, but clear on exfoliated specimens, scarcely noticeable when the test is preserved. Brim simple, flat, and owing to the slight divergence of the anterior sutures, longer than glabella. In exfoliated specimens a slightly thickened rim is margined in the rear by a row of tubercles. Fixigenes narrow. Eyes situated about the middle of the head, palpebral lobes not separated by furrow or direction of slope from the fixigene.

The pygidium is similar to that of *Taenicephalus* but has a variable number of marginal spines.

Outer test evidently smooth except for striations toward the margins. Exfoliated specimens are sparsely granulose, in addition to the mentioned row of tubercles along the anterior furrow. Further, the preglabellar area is vertically lined in such specimens. Libragenes with long spines, striated on their outer surface.

*Genotype*.—*Ptychoparia llanoensis* Walcott.

*Name*.—ὄρυγμα = pit; ασπίς = shield.

**Orygmaspis llanoensis (Walcott)**

*Ptychoparia llanoensis* WALCOTT, Proc. U. S. Nat. Mus., vol. 13, p. 272, pl. 21, figs. 3-5, 1890; U. S. Geol. Surv. Mon. 32, pt. 2, p. 458, pl. 64, fig. 4, 1899.

*Conaspis llanoensis* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 358, 1914.

Upper Cambrian, Wilberns; (loc. 68) Packsaddle Mountain, 11 miles southeast of Llano, Texas.

*Cotypes*.—U.S.N.M. no. 23857.

**Orygmaspis eryon (Hall)**

*Conoccephalites eryon* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 157, pl. 7, figs. 10-16, 1863.

*Conaspis eryon* HALL, idem, p. 152, 1863.

*Conaspis eryon* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 358, 1914.

Upper Cambrian, Franconia; Trempealeau, and other localities in Wisconsin.

*Cotypes*.—A.M.N.H. no. 327; casts, U.S.N.M. no. 89936; meta-types, U.S.N.M. no. 10011.

**PERIOMMA Resser, 1936****Periomma leuka (Walcott)**

*Olenopsis leuka* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 77, pl. 13, fig. 4, 1917.

This species is not quite typical of the genus, but the extra width of the brim may be attributable to the coarse matrix.

Lower Cambrian, Mount Whyte; (loc. 58g) Mount Bosworth, British Columbia.

*Holotype*.—U.S.N.M. no. 64397.

**Periomma cilles (Walcott)**

*Ptychoparia ? cilles* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 2, p. 32, pl. 6, fig. 2, 1917.

Lower Cambrian, Mount Whyte; (loc. 63d) Ptarmigan Peak, northeast of Lake Louise, Alberta.

*Holotype*.—U.S.N.M. no. 63737.

**PLAGIURELLA, n. gen.**

Small trilobites which have the same general aspect as *Plagiura* in that the facial suture has such a strong converging direction forward, seem to require separate generic recognition.

*Diagnosis*.—Small trilobites. Glabella long, rather slender, gently tapered, rounded in front. Glabellar furrows faintly indicated. Neck furrow deep and neck ring expanded into short, blunt spine. Facial suture converges slightly anterior to the eyes, but back of them diverges rapidly to form very large posterolateral limbs. Eyes small, situated close to the anterior end of glabella. Eye lines rather strong, with a horizontal course. Brim with a narrow preglabellar area, and thickened, somewhat upturned rim.

Compared with *Plagiura* the new genus had deeper furrows throughout, and also has a raised rim.

*Range*.—Lower Cambrian, Cordilleran and Appalachian regions.

*Genotype*.—*Ptychoparia* ? *cleadas* Walcott.

**Plagiurella cleadas (Walcott)**

*Ptychoparia* ? *cleadas* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 83, pl. 12, fig. 2, 1917.

Lower Cambrian, Mount Whyte; (loc. 57s) Mount Bosworth, Alberta.

*Holotype*.—U.S.N.M. no. 64382.

**POULSENIA Resser, 1936**

**Poulsenia cossus (Walcott)**

*Ptychoparia cossus* WALCOTT, Smithsonian Misc. Coll., vol. 67, no. 3, p. 86, pl. 11, figs. 5, 5a, 1917.

Lower Cambrian, Mount Whyte; (loc. 61a) Yoho Canyon, British Columbia.

*Holotype*.—U.S.N.M. no. 64370.

**Poulsenia crassilimbata (Poulsen)**

*Elrathia* ? *crassilimbata* POULSEN, Meddels. Grønland, vol. 70, p. 274, pl. 17, figs. 5, 6, 1927.

Middle Cambrian, Cape Wood; Cape Frederick VII, northwest Greenland.

*Holotype*.—Min. Mus. Copenhagen.

**PROZACANTHOIDES, n. gen.**

*Diagnosis*.—Glabella large, occupying the major portion of the cranidial length, rectangular in shape, with a tendency to expand forward. Three pairs short glabellar furrows, the anterior pair very faint and the rear pair sharply reflexed. Occipital furrow straight and clearly impressed; occipital spine present. Fixed cheeks confined to the large palpebral lobes and small lobes anterior to the eyes. Facial

suture rather strongly divergent anterior to the eyes. Eyes large, extending forward from the occipital furrow. Brim concave, with a narrow rim sometimes demarcated.

Libragenes, hypostoma and thorax unknown.

Pygidium with a prominent axis, rather wide and highly arched, terminated bluntly or with a postaxial ridge. Pleural lobes flat, pleura turning sharply backward and ending in blunt spines; usually well fused but with the pleural grooves showing.

Compared with *Zacanthoides*, *Prozacanthoides* is constructed on a similar plan but the glabella expands forward and the pygidial axis does not take up as much of the total area. In addition the pleura are less fused, remaining more like those of an ordinary trilobite.

*Genotype*.—*Olenoides stissingensis* Dwight.

Numerous species occur in the Lower Cambrian of the Appalachians.

***Prozacanthoides stissingensis* (Dwight)**

*Olenoides stissingensis* DWIGHT, Amer. Journ. Sci., 3d ser., vol. 38, p. 147, pl. 6, figs. 9-15, 1889; Vassar Bros. Inst., vol. 5, p. 105, pl., figs. 9-15, 1890.

Lower Cambrian; Stissing, Dutchess County, New York.

*Cotypes*.—U.S.N.M. no. 18365.

***Prozacanthoides charilla* (Walcott)**

*Zacanthoides charilla* WALCOTT (part), Smithsonian Misc. Coll., vol. 67, no. 2, p. 40, pl. 6, fig. 9a, 1917 (not fig. 9 = *Clavaspidella sylia*).

Middle Cambrian, Chetang; (loc. 61 o) Chetang Cliffs, 7 miles northeast of Robson Peak, Alberta.

*Holotype*.—U.S.N.M. no. 63753.

**PSALASPIS, n. gen.**

*Diagnosis*.—Peculiar trilobite of about average size. Strongly convex longitudinally and including the libragenes, also in the opposite direction. Glabella tapered, a little more than half the length of the head; conforming in convexity to the cranium and only outlined by the rather weak dorsal furrow; weak glabellar furrows present; glabella keeled. Brim single, convex and turned downward. Fixigenes narrow. Eyes small, situated behind the middle of the head.

Libragenes evenly and highly convex, without rim and with a weak occipital furrow, extended into very long recurved genal spines.

*Genotype*.—*Conocephalites patersoni* Hall.

*Name*.—ψαλς = arch; ασπίς = shield.

***Psalaspis patersoni* (Hall)**

*Conocephalites patersoni* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 159, pl. 7, figs. 45, 46, 1863.

*Conaspis patersoni* HALL, idem, p. 152.

*Conaspis patersoni* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 358, 1914.

Upper Cambrian, Franconia; Trempealeau, and other localities, Wisconsin; Reads Landing, Minnesota.

*Cotypes*.—A.M.N.H. no. 328.

**PTYCHOPARELLA Poulsen, 1927*****Ptychoparella canadensis* (Kobayashi)**

*Chancia canadensis* KOBAYASHI, Journ. Pal., vol. 10, no. 3, p. 164, pl. 21, fig. 28, 1936.

Middle Cambrian; Cap Mountain Ridge, Mackenzie District, Canada.

*Holotype*.—Nat. Mus. Canada no. 8714.

**SAUKIELLA Ulrich and Resser, 1933*****Saukiella fallax* (Walcott)**

*Saukia fallax* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 378, pl. 67, figs. 21-22a, 1914.

Upper Cambrian, Wilberns; (loc. 70a) 8 miles northwest of Burnet, Texas.

*Cotypes*.—U.S.N.M. no. 58647.

**STIGMACEPHALUS, n. gen.**

In breaking up the *Conaspis* group, it is easy to remove the several diverse forms. One of these, characterized below, lies between *Conaspis* and the radically different genus *Monocheilus*.

*Diagnosis*.—Rather small trilobites with large glabella. Glabella occupies three-fourths the length of the head, tapered slightly, rounded in front, and usually with pits in the anterior angles of the dorsal furrows. Glabellar furrows practically absent. Brim convex and turned downward, and with only a faint anterior furrow, which involves no change in the slope of the brim. Fixigenes narrow; eyes small, situated about the middle of the head. Libragenes rather large, evenly convex and with stout, long genal spines.

*Genotype*.—*Conocephalites oweni* Hall.

*Name*.—στῆγμα = puncture; κεφαλος = head.



**Stigmacephalus oweni (Hall)**

*Conocephalites oweni* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 155, pl. 8, figs. 17, 20, 1863.

*Conaspis oweni* HALL, idem, p. 152, 1863.

*Conaspis oweni* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 357, 1914.

Upper Cambrian, Franconia; Marine Mills, Minnesota, and localities in Wisconsin.

*Cotypes*.—A.M.N.H. no. 318; *topotypes*, U.S.N.M. no. 10018.

**Stigmacephalus bipunctatus (Shumard)**

*Arionellus bipunctatus* SHUMARD, Trans. Acad. Sci. St. Louis, vol. 2, p. 101, 1862.

*Arionellus bipunctatus* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 169, pl. 7, figs. 50, 51, 1863.

*Conaspis bipunctata* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 358, 1914.

Upper Cambrian, Franconia; Lawrence Creek, St. Croix River and Root River, Minnesota, and localities in Wisconsin.

*Cotypes*.—(Hall's figures are likely from Shumard's specimens) (Plesiotypes?) A.M.N.H. 337; *metatypes*, U.S.N.M. no. 10007.

**TAENICEPHALUS Ulrich and Resser, 1924****Taenicephalus nasutus (Hall)**

*Conocephalites nasutus* HALL, 16th Ann. Rep. New York State Cab. Nat. Hist., p. 155, pl. 7, figs. 3-9, 1863.

*Conaspis nasuta* HALL, idem, p. 152, 1863.

Upper Cambrian, Franconia; Kickapoo and other localities in Wisconsin.

*Cotypes*.—A.M.N.H. no. 313 (casts, U.S.N.M. no. 89938); *metatypes*, U. S. N. M. no. 10014.

**TELLERINA Ulrich and Resser, 1933****Tellerina marica (Walcott)**

*Dicelloccephalus marica* WALCOTT, U. S. Geol. Surv. Mon. 8, p. 44, pl. 10, fig. 13, 1884.

*Saukia marica* WALCOTT, Smithsonian Misc. Coll., vol. 57, no. 13, p. 380, pl. 64, figs. 6, 6a, 1914.

This species is not fully typical of *Tellerina* because of the greater width of the fixigene at the anterior end of the eye lobe. However, it seems undesirable to make a new genus for this species now. If these specimens come from the Secret Canyon formation, this becomes the oldest known species of *Tellerina*.

Upper Cambrian, Secret Canyon; (loc. 62) Canyon north of Adams Hill, Eureka District, Nevada.

*Holotype*.—U.S.N.M. no. 24565.

**TRICREPICEPHALUS** Kobayashi, 1936**Tricrepicephalus yellowstonensis**, n. sp.

*Crepicephalus texanus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 3, p. 209, pl. 30, figs. 4, 4a, 1916.

Compared with *T. tripunctatus*, the similar species in the region, *T. yellowstonensis* differs first in having fewer granules on the brim and behind the eyes on the fixigenes, and practically none on the glabella. A further very conspicuous difference is the evenness of rim width due to lack of a forward projection in the middle.

Upper Cambrian, Pilgrim; (loc. 151b) between Pebble and Soda Butte Creeks, northeastern Yellowstone Park, Montana.

*Holotype and paratype*.—U.S.N.M. no. 61523.

**Tricrepicephalus beltensis**, n. sp.

*Crepicephalus texanus* WALCOTT (part), Smithsonian Misc. Coll., vol. 64, no. 3, p. 209, pl. 29, fig. 7, 1916.

In general appearance this species resembles *T. yellowstonensis*. It differs in being less convex in both directions but more particularly in the practically even distribution of granules over the entire cranium.

Upper Cambrian, Pilgrim; (loc. 151i) Smith River, 6 miles north-east of White Sulphur Springs, Montana.

*Holotype*.—U.S.N.M. no. 61644.

**WHITFIELDINA**, n. gen.

This peculiar small trilobite is evidently rather rare, although one hand specimen contains more than five cranidia.

*Diagnosis*.—Glabella quadrate, about half the length of the head, and extends back of the rear margin, without an occipital furrow, the glabella itself tapering to the base of a long, slender spine. Brim wide, with a wide convex preglabellar area and an upturned rim. Fixigenes nearly as wide as the glabella. Eyes small, situated about the middle of the head.

*Genotype*.—*Conocephalites quadratus* Whitfield.

**Whitfieldina quadrata** (Whitfield)

*Conocephalites quadratus* WHITFIELD, Ann. Rep. for 1879, Wisconsin Geol. Surv., p. 47, 1880; Geol. Wisconsin, vol. 4, p. 180, pl. 1, figs. 15, 16, 1882. *Ptychoparia quadrangularis* VODGES, California Acad. Sci. Occ. Papers, vol. 4, p. 353, 1893.

*Ptychoparia* ? *quadrata* MILLER, N. A. Geol. p. 565, 1889.

Upper Cambrian, Eau Claire, (Cedaria zone); Eau Claire and other localities, Wisconsin.

*Cotypes*.—Univ. Wisconsin.

## WILBERNIA Walcott, 1924

**Wilbernia diademata (Hall)**

*Conocephalites diadematus* HALL (part), 16th Ann. Rep. New York State Cab. Nat. Hist., p. 167, pl. 7, fig. 36; pl. 8, fig. 21, 1863 (not pl. 7, figs. 37, 38 = *W. halli*; pl. 8, fig. 18 = indeterminate fragment).

Hall's figure is not accurate, particularly in the restoration of the eye lobes.

Upper Cambrian, Franconia; Marine Mills, Minnesota.

*Cotypes*.—A.M.N.H.; cast cranidium, U.S.N.M. no. 89953; meta-types, U.S.N.M. no. 10010.

**Wilbernia halli, n. sp.**

*Conocephalites diadematus* HALL (part), see above.

*Dicellocephalus misa* BERKEY, Amer. Geol., vol. 21, p. 290, pl. 20, figs. 12, 13, 1898.

Compared with *W. diademata*, this species is wider, has a wider preglabellar area, and the rim is more upturned.

Upper Cambrian, Franconia; Root River, and Franconia, Wisconsin.

*Cotypes*.—A.M.N.H.; plesiotype, Columbia Univ.

**Wilbernia walcotti, n. sp.**

*Ptychoparia* ? *diademata* WALCOTT (part), U. S. Geol. Surv. Mon. 32, p. 462, pl. 64, figs. 2-2b, 1899 (not 2c = *W. hudsonensis* from Wisconsin).

This species is more like the genotype *W. pero* in its curved outline and size. It, however, has a narrower preglabellar area and somewhat wider rim.

Upper Cambrian, Dry Creek; Soda Butte Creek, Yellowstone National Park, Wyoming.

*Cotypes*.—U.S.N.M. no. 35227.

**Wilbernia hudsonensis, n. sp.**

*Ptychoparia* ? *diademata* WALCOTT (part), U. S. Geol. Surv. Mon. 32, p. 462, pl. 64, fig. 2c, 1899.

Unfortunately, this specimen was never properly labeled, for which reason it is necessary to choose from the specimens on hand from the locality. One pygidium has the same green marks as on the Yellowstone specimens figured at the same time, and likely is the holotype. At any rate it agrees with the drawing, except for obvious restoration.

*W. hudsonensis* is larger than any described species, but is particularly characterized by the straight course and considerable depth of the pleural furrows and grooves and its transverse anterior margin.

Upper Cambrian, Franconia; (loc. 79) Hudson, Wisconsin.

*Holotype*.—U.S.N.M. no. 35228.

## ZACANTHOIDES Walcott, 1888

*Zacanthoides weedi*, n. sp.

*Zacanthoides* sp. WALCOTT, U. S. Geol. Surv. Mon. 32, p. 465, pl. 65, fig. 3, 1899.

This small form is characterized by its reduced rim and furrows (drawn too heavily in the above cited figure). It is possible that when the pygidium is found it will prove to belong to *Prozacanthoides*. It is associated with *Kootenia*.

Middle Cambrian, Meagher; (loc. 151d) Crowfoot Ridge, Yellowstone National Park, Wyoming.

*Holotype*.—U.S.N.M. no. 94345.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

VOLUME 95, NUMBER 23

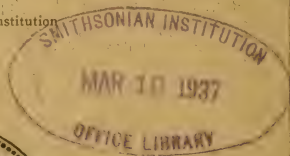
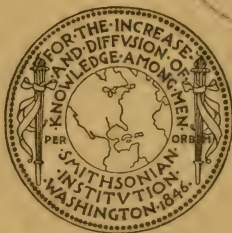
## Roebbling Fund

# ON THE CORRECTIONS TO BE APPLIED TO SILVER-DISK PYRHELIOMETRY

BY

C. G. ABBOT

Secretary, Smithsonian Institution



(PUBLICATION 3409)

CITY OF WASHINGTON

PUBLISHED BY THE SMITHSONIAN INSTITUTION

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### ON THE CORRECTIONS TO BE APPLIED TO SILVER-DISK PYRHELIOMETRY

By C. G. ABBOT

*Secretary, Smithsonian Institution*

In the *Zeitschrift für Meteorologie* for October 1936, Fuessner has presented evidence which convinced him that the correction factors K and K' given in association with silver-disk pyrhelimeters are inapplicable, and better omitted. If this were true, it would overthrow the results of 25 years of observing, as published in the *Annals of the Astrophysical Observatory*, and in my recent papers on the dependence of weather on variations of solar radiation.<sup>1</sup>

The following facts contradict Fuessner's conclusion:

1. If the corrections had been omitted in reducing pyrhelimetry at Montezuma, Chile, with silver-disk pyrhelimeters S. I. 30 and S. I. 31, certain notable changes would have occurred in the solar-constant values reported in table 31, volume 5, *Annals of the Astrophysical Observatory*. To fix ideas I will first refer to these *Annals*, volume 5, pages 69, 211, and 213. From these references we note that in the months of August and November, 1929 and 1930, the average temperature of the air at 8 o'clock a. m. (which can have differed but little from that at which the pyrhelimeters were read) was higher by 15° F. in 1929 and by 12° F. in 1930 in November than in August. Transforming these differences to Centigrade and performing the appropriate computations, it appears that the omission of the correction factors would have produced a change in the relative values of the mean solar-constant numbers for these two months of approximately 0.019 calorie in 1929, and 0.016 calorie in 1930. The actual monthly means of the solar-constant values as given on pages 211 and 213 for Montezuma observations were 1.931 and 1.936 in the year 1929, and 1.945 and 1.944 in the year 1930. To speak approximately, the published difference of only 0.005 calorie in 1929 would have become 0.024 calorie, and the published difference of only 0.001 calorie in 1930 would have become 0.015 calorie if the silver-disk pyrhelimeter corrections had been omitted.

<sup>1</sup> *Smithsonian Miscellaneous Collections*, vol. 94, no. 10, 1935; vol. 95, nos. 12, 15, 19, 1936.

Again, referring to page 252, *Annals*, volume 5, consider the third line of the first table. The average yearly range from winter to summer of the published mean solar-constant values observed at Montezuma in the period of 10 years from 1921 to 1930 is only from 1.9397 calories (the 10-year mean, June to August) to 1.9398 (the 10-year mean, December to February). If the silver-disk pyrheliometer correction factors were omitted, we see from page 69, and from the

TABLE I

*Group A*

Dates		1935 June 23	June 26	July 13	Aug. 8	Aug. 9	Aug. 16	Aug. 17		Mean Diff.
Mean Bulb Temps. C.	Montezuma...	19°.5	16°.8	17°.3	18°.9	21°.3	18°.4	16°.2		
	St. Katherine.	24°.0	22°.9	22°.2	20°.0	28°.3	26°.8	28°.4		
	Difference....	- 4°.5	- 6°.1	- 4°.0	-10°.1	- 7°.0	+ 8°.4	-12°.2		- 7°.6
Solar Const.	Montezuma...	42 S - 41 S	37 S - 43 S	44 S 35 S	44 S - 43 S	43 S - 43 S	48 S - 45 S	32 S - 46 S		
	St. Katherine.									
Montez. minus St. Kath.	Actual.....	+ 1	- 4	+ 9	+ 1	0	+ 3	-14		- 1
	Without correction..	+11	+ 9	+19	+23	+15	+21	+12		+16

*Group B*

Dates		1934 Dec. 5	Dec. 17	1935 Jan. 2	Jan. 6	Jan. 10	Feb. 15	Feb. 22	Nov. 15	
Mean Bulb Temps. C.	Montezuma...	24°.7	24°.1	20°.7	21°.3	23°.9	23°.2	24°.6	23°.1	
	St. Katherine.	13°.4	14°.2	6°.3	10°.4	14°.2	12°.1	10°.0	15°.9	
	Difference....	+11°.3	+ 9°.9	+14°.4	+10°.9	+ 9°.7	+11°.1	+14°.6	+ 7°.2	+11°.1
Solar Const.	Montezuma...	51 S - 46 S	56 S - 50 S	46 S - 48 S	49 S - 46 S	42 S - 35 S	49 S - 42 S	42 S - 52 S	53 S - 45 S	
	St. Katherine.									
Montez. minus St. Kath.	Actual.....	+ 5	+ 6	- 2	+ 3	+ 7	+ 7	-10	+ 8	+ 3
	Without correction..	-19	-15	-33	-20	-14	-17	-41	-7	-21

figures just given above, that for the 10-year averages instead of a yearly range of 0.0001 calorie (or 5/1000 percent) the solar-constant values would have shown an approximate average yearly range from winter to summer of about 0.0180 calorie (or almost an entire 1 percent).

These facts alone show strongly indirect evidence that it is very improbable that the application of the silver-disk correction factors can properly be omitted.

2. We have now two first-rate solar stations, Montezuma and St. Katherine, which lie in opposite hemispheres. Summer at the one comes during the winter at the other. My colleague, L. B. Aldrich, has collected for me groups of solar-constant values of two kinds (table 1). In the one kind, group A, it was winter at Montezuma and summer at St. Katherine. In the other kind, group B, it was summer at Montezuma and winter at St. Katherine. We shall now see what the actual mean values of the solar constant were found to be at the two stations and what they would have been found to be if the silver-disk pyrhelimeter correction factors had been omitted. The solar-constant values given are all to be understood as prefixed with 1.9. Thus for 42 read 1.942. They are not absolutely final values, as we are still engaged in removing small sources of error before final publication, but they are the best we now have.

From these typical good days it is seen that with an average temperature difference between group A and group B of  $-18^{\circ}7$ , the actual mean difference of solar-constant values was  $-0.004$  calorie, or 2/10 percent. Had the pyrhelimeter corrections been omitted it would have been  $+0.037$  calorie, or 2 percent, a discrepancy 10 times as large.

3. The correction factors  $K$  and  $K'$  to the silver-disk pyrhelimetry were not guessed at. As regards  $K$ , they were the results of observation, as regards  $K'$ , of well-accepted principles of exact thermometry.

As for the factor  $K$ :

In the years 1910 and 1911, L. B. Aldrich and the writer compared silver-disk pyrhelimeters S. I. 1, S. I. 2, S. I. 3, S. I. 4, A. P. O. 8, and A. P. O. IV on several different days with temperatures ranging from  $11^{\circ}$  C. to  $43^{\circ}5$  C. The instruments were repeatedly interchanged as regards temperature. I will omit details, as I shall give below a later comparison made in the same way.

A general summary of all of these experiments of the years 1910 and 1911 is as follows:

TABLE 2

Comparisons of pyrhelimeters	Number	Value of $K$	Assumed weight
S. I. 1 with A. P. O. 8	11	$-0.00111$	2
S. I. 2    "    "    "	10	$-0.00132$	2
S. I. 3    "    "    "	10	$-0.00104$	3 <sup>a</sup>
S. I. 4    "    "    "	10	$-0.00034$	1/2 <sup>a</sup>
A. P. O. IV with A. P. O. 8	9	$-0.00108$	2
Weighted mean		$-0.00109$	
Adopted value		$-0.0011$	

<sup>a</sup> The higher weight given S. I. 3 with A. P. O. 8, and the lower weight given S. I. 4 with A. P. O. 8, depended principally on the wide temperature differences with the former pair, and the narrow temperature differences which happened to have prevailed with the latter pair.



As for the factor  $K'$ :

When exposure to the sun drives mercury into the capillary of the thermometer, the length of the column of newly appearing mercury depends on the temperature prevailing in the thermometer stem. The coefficient of linear expansion of mercury in a capillary of the glass used in the thermometer may be taken as 0.00014 per degree Centigrade. The rise of temperature of the pyrhelimeter is therefore corrected to what it would have been at a stem temperature of  $20^{\circ}\text{C.}$ , namely, by the corrected temperature rise multiplied by  $0.00014(20^{\circ} - T)$ .

4. The indirect and direct evidence I have thus far brought forward seems to me more weighty than that which moved Fuessner to his conclusion. For his observations involved the peculiarities of several other types of pyrhelimeters and were made in a high latitude at rather low sun. Yet since, if sustained, Fuessner's conclusion invalidates nearly the whole program of the Smithsonian Astrophysical Observatory for the past 25 years, I have felt it to be necessary to redetermine the factor  $K$  from new observations. For this purpose I directed Messrs. Zodtner and Greeley, both highly skilled observers of long experience, now operating our station at Table Mountain, California, to make numerous direct comparisons of silver-disk pyrhelimeters A. P. O. 10 and A. P. O. 12, using pendulum beats to fix the times of observing. Their program is as follows:

Observing in a warm room with opened window with one pyrhelimeter, and immediately outside in winter's cold with the other, a series of absolutely simultaneous comparisons is made. Time signals for both observers were given by a pendulum. Then, without removing the instruments, they are allowed to return to nearly the temperatures of their respective surroundings, and a second comparison is made with exchanged observers. Then, on a second day, or later in the same day, with the instruments exchanged, so that that which was warm has now become cold, and that which was cold has now become warm, the same program is repeated. In this way the instruments and the observers were exchanged again and again, until satisfactory results had been obtained. These observations were made in good sky conditions with fairly high sun at the latitude  $34^{\circ}$  North.

As the matter is of importance to support the accuracy of the last 25 years of work of the Astrophysical Observatory, I give the results in some detail. In the following table the readings marked  $R$  represent the corrected rise of temperature of the pyrhelimeter after proper corrections are applied for irregularity of the bore of the stem and for reducing the temperature of the stem to  $20^{\circ}\text{C.}$

TABLE 3

Jan. 21, 1937. F. A. G. reading A. P. O. 12, H. H. Z. reading A. P. O. 10.

A. P. O. 12		A. P. O. 10		$\Delta T$	$\Delta R$	$\Delta \Delta T$	$\Delta \Delta R$	K
Bulb temp. T	Corrected R	Bulb temp. T	Corrected R					
10.8	4.373	-1.6	4.591	-12.4	0.218			
14.8	4.369	+1.3	4.583	-13.5	0.214			
17.1	4.370	+2.5	4.611	-14.6	0.241			
17.4	4.361	+1.4	4.625	-16.0	0.244			

Jan. 26, 1937. F. A. G. reading A. P. O. 12, H. H. Z. reading A. P. O. 10.

6.3	4.307	14.0	4.398	7.7	0.091	-20.1	0.127	-0.00140
9.1	4.312	18.5	4.437	9.4	0.125	-22.9	0.080	-0.00086
10.4	4.317	22.0	4.442	11.6	0.125	-26.2	0.116	-0.00098
11.0	4.312	24.6	4.438	13.6	0.126	-29.6	0.118	-0.00091

Jan. 21, 1937. H. H. Z. reading A. P. O. 12, F. A. G. reading A. P. O. 10.

17.9	4.337	1.3	4.583	-16.6	0.246			
17.9	4.326	0.7	4.568	-17.2	0.242			
18.9	4.430 ?	1.7	4.588	-17.2	0.158 ?			
19.3	4.394	2.3	4.604	-17.0	0.210			

Jan. 26, 1937. H. H. Z. reading A. P. O. 12, F. A. G. reading A. P. O. 10.

7.8	4.352	28.3	4.426	20.5	0.074	-37.1	0.172	-0.00103
9.5	4.363	31.8	4.398	22.3	0.035	-39.5	0.207	-0.00117
10.2	4.368	34.4	4.392	24.2	0.024	-41.4	0.134 ?	-0.00067 ? <sup>a</sup>
10.5	4.348	36.4	4.404	25.9	0.056	-42.9	0.154	-0.00080

Jan. 26, 1937. H. H. Z. reading A. P. O. 12, F. A. G. reading A. P. O. 10.

13.8	4.456	26.9	4.353	13.1	-0.103			
19.3	4.335	26.2	4.368	6.9	+0.033			
23.2	4.324	24.9	4.375	1.7	0.051			
25.9	4.277	23.7	4.397	-2.2	0.120			
28.1	4.205	22.8	4.320	-5.3	0.115			

Jan. 27, 1937. H. H. Z. reading A. P. O. 12, F. A. G. reading A. P. O. 10.

24.3	4.256	19.2	4.407	-5.1	0.151	18.2	-0.254	-0.00320 <sup>a</sup>
26.8	4.265	19.1	4.387	-7.7	0.122	14.6	-0.089	-0.00139
28.6	4.252	18.9	4.403	-9.7	0.151	11.4	-0.100	-0.00201 <sup>a</sup>
29.9	4.241	18.7	4.394	-11.2	0.153	9.0	-0.033	-0.00108
30.3	4.214	18.5	4.389	-11.8	0.175	6.5	-0.060	-0.00121

Jan. 26, 1937. F. A. G. reading A. P. O. 12, H. H. Z. reading A. P. O. 10.

28.1	4.075	17.0	4.237	-11.1	0.162			
30.6	4.071	18.3	4.237	-12.3	0.166			
31.9	3.983	18.6	4.224	-13.3	0.241			
33.0	3.944	17.4	4.141	-15.6	0.197			

Feb. 1, 1937. F. A. G. reading A. P. O. 12, H. H. Z. reading A. P. O. 10.

10.2	4.456	17.8	4.498	7.6	0.042	-18.7	0.120	-0.00147
10.7	4.401	24.1	4.508	13.4	0.107	-25.7	0.059	-0.00053 <sup>a</sup>
12.6	4.381	28.4	4.485	15.8	0.104	-29.1	0.137	-0.00108
13.4	4.406	31.4	4.496	18.0	0.090	-33.6	0.107	-0.00073

General mean (13 values) -0.00109

<sup>a</sup> These 4 values omitted from the mean. Their mean is -0.00160.

The reader will notice that by the method of reduction adopted, whereby for every determination the same instrument is read both warm and cool by the same observer, and the results thus obtained are subtracted, personal equation is eliminated and it is not necessary to know the reduction factors applicable to the instruments compared. The result  $K=0.00109$  is identical with that found by Abbot and Aldrich 25 years ago, and indicates no desirable correction to the published preferred value,  $K=0.0011$ .

5. Although our coefficient as heretofore published appears to be applicable to the measurements of the 11 silver-disk pyrheliometers referred to in this paper, some one may raise the question as to whether it is applicable to the instrument S. I. 12 at Potsdam which was employed by Fuessner. Inasmuch as all of the pyrheliometers we have prepared and sent out from the Smithsonian Institution are made of similar materials, and with their receivers of identical sizes, it is highly improbable that the Potsdam pyrheliometer is exceptional.

But there is a further check on this question. In October 1931 the writer carried silver-disk pyrheliometer S. I. 5<sub>bis</sub> to Potsdam, and at 2 separate times involving a considerable range of temperatures, comparisons were made between it and the Potsdam instrument S. I. 12. The results were uncommonly harmonious, as both instruments were reduced with the usual value of the temperature coefficient  $K$ . Hence we may believe that as concerns temperature these two instruments, S. I. 5<sub>bis</sub> and S. I. 12, are alike. But in 1932 and 1934, silver-disk pyrheliometer S. I. 5<sub>bis</sub> was carefully compared with the new water-flow double-chamber standard pyrheliometer No. 5 on Mount Wilson. These comparisons involved a range of temperature from 26° to 46° C. We were unable to detect any differences in results showing the influence of this large range in temperatures. Had the coefficient  $K$  been omitted, as recommended by Fuessner, a progressive range of 2.2 percent would have appeared. Hence we may be sure that S. I. 5<sub>bis</sub> is no exception in temperature behavior to the 11 others referred to in this paper, and the Potsdam comparison indicates that the instrument S. I. 12 used in Fuessner's investigations behaved similarly.

*Conclusion.*—I do not think it devolves on me to suggest what conditions of instruments or observation may have led Fuessner to the false conclusion he has published that the temperature coefficients should be omitted from reductions of measurements with the silver-disk pyrheliometers. I feel sure that if he had reflected that such a change would destroy all of the conclusions on solar variability and its consequences which have come from the work of the Astrophysical

Observatory for 25 years, he would have been kind enough to have consulted me privately before publishing his conclusion. The prolonged hurtful influence of such an important erroneous publication in the literature can never be overtaken by any subsequent correction. However, copies of the present paper will be sent to all owners of silver-disk pyrheliometers, and to many other individuals and institutions likely to be interested.

I must add that since the work published by Fuessner on the absolute scale of pyrheliometry is certainly vitiated so far as it depends on his preferred reduction of the silver-disk pyrheliometer observations, and was moreover of a character that permitted so erroneous a conclusion to be derived as that which he has published, I cannot but feel that its findings as to absolute pyrheliometry must be taken with great reserve. It would be very desirable indeed if a direct comparison could be made at Mount Wilson between the Smithsonian water-flow double-chamber pyrheliometer No. 5, and the standard pyrheliometer which was employed by Fuessner.



SMITHSONIAN MISCELLANEOUS COLLECTIONS

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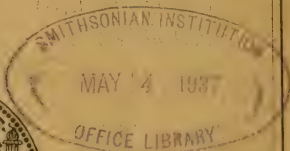
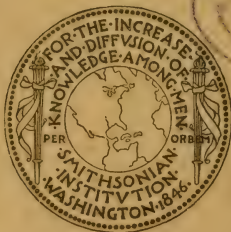
# TIME COURSE OF PHOTOSYNTHESIS FOR A HIGHER PLANT

(WITH TWO PLATES)

BY

E. D. McALISTER

Division of Radiation and Organisms,  
Smithsonian Institution



(PUBLICATION 3410)

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By E. D. McALISTER

*Division of Radiation and Organisms, Smithsonian Institution*

(WITH TWO PLATES)

A spectrographic (infrared) method of carbon dioxide determination of unique speed and sensitivity has been developed. It has the additional merits of being independent of water vapor and of having small pressure and temperature corrections. At low concentrations the method will detect one part of carbon dioxide gas to a million parts of air. Without a great loss in sensitivity these measurements may be made in a fraction of a second. By changing the wave length of radiation used, other gases may be similarly observed. For example, by using radiation of wave lengths absorbed by water vapor the transpiration of a plant may be studied with equal success. Because of its speed, the method is particularly useful in following the time course of a gaseous exchange. In this connection it could be arranged to measure the metabolic ratio for each breath taken by an animal.

The purpose of this paper is to report results obtained by the application of this method to measurements of the carbon dioxide exchange between a higher plant (wheat, variety Marquis) and its surroundings.

The data obtained by Hoover, Johnston, and Brackett (1933) on the carbon dioxide assimilation of young wheat plants (variety Marquis) as a function of light intensity and carbon dioxide concentration are the most accurate and self-consistent so far reported. Figure 1 is one of their families of assimilation curves. The precision and reproducibility here shown justify their concluding sentence: "These experiments indicate that a wide range of critical experiments upon photosynthesis may be carried out with higher plants. . . ." The present experiments on the same organism bear out this conclusion and bring forth much new information.

It is a pleasure for the writer to acknowledge his indebtedness to Dr. C. G. Abbot for his constant interest and enthusiastic support; to Dr. Earl S. Johnston for many helpful suggestions on the plant physiological side of this work; and to Dr. Dean Burk for many stimulating discussions.

## EXPERIMENTAL

Since the method of measuring carbon dioxide used in the present experiments is new, it will first be very briefly described. The method is based upon the experimental fact that carbon dioxide gas is a very powerful absorber of a certain band of infrared radiation. Two millimeters thickness of pure carbon dioxide at N. T. P. absorb 78 per cent of the radiation in a band from  $4.2$  to  $4.3\ \mu$ . Thus in a long optical path, small concentrations of carbon dioxide will cause marked absorption of this radiation. No other gas or vapor, including water

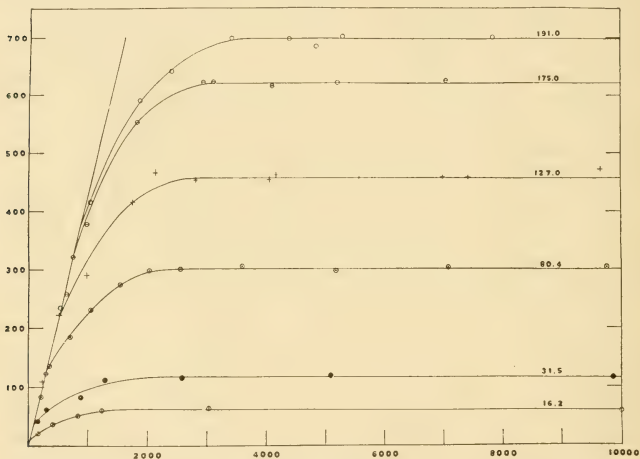


FIG. 1.—Carbon dioxide assimilation curves. (After Hoover, Johnston, and Brackett.) Ordinates, carbon dioxide assimilated. Multiply by 0.25 to obtain cubic millimeters per minute. Abscissae, carbon dioxide concentration. Multiply by  $41 \times 10^{-6}$  to obtain volume percent. Parameters, light intensities. Multiply by  $3.56 \times 10^{-4}$  to obtain watts/cm<sup>2</sup>, or by 4.96 to obtain foot-candles.

vapor, common to air absorbs this band of radiation. Hence the method is specific for carbon dioxide alone, and is not affected by humidity changes. Because of its nature, the method has almost negligible temperature and pressure corrections. It is as sensitive as the best chemical methods since at small concentrations it will detect one part in a million (by volume) of carbon dioxide. It is practically instantaneous, the response of the galvanometer-thermocouple system (about 5 seconds) determining this. Because of this latter fact, for most purposes it is many times more sensitive than any chemical method, since it will detect this one-millionth part of carbon dioxide in 5 seconds.

Figure 2 shows a diagram, and plate 1 a photograph, of the plant-growth chamber, air-conditioning system, and optical absorption tube wherein the carbon dioxide is measured. This tube provides an optical path of about 1 meter. The growth chamber has a water jacket which provides constant "surroundings" for the plant. The water in this jacket has the same temperature as the incoming air, since it

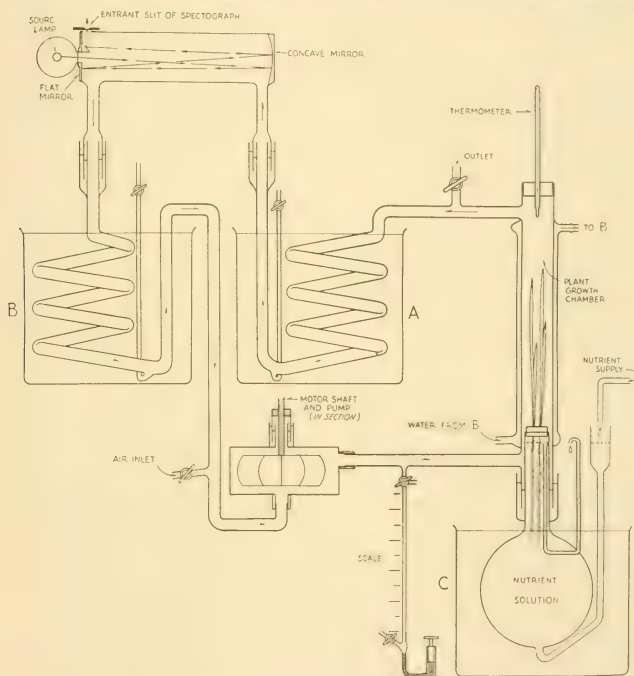


FIG. 2.—Plant growth chamber and accessory system.

flows from bath B. Bath A is held  $3^{\circ}$  C. below B to provide constant humidity. For simplicity's sake the temperature controls in baths A, B, and C (C provides root temperature control) are not shown. The spectrograph used has halite (rock salt) optics and is of numerical aperture about F-8. The vacuum thermocouple (located at the exit slit of the spectrograph and reading on the  $4.2\text{--}4.3\ \mu$  band) and galvanometer used provide a sensitivity of from 2 to 5 ten-thousandths



of 1 percent carbon dioxide, depending on the concentration in the system, for 1 millimeter deflection. Calibration is accomplished by inserting known amounts of pure carbon dioxide into the system by

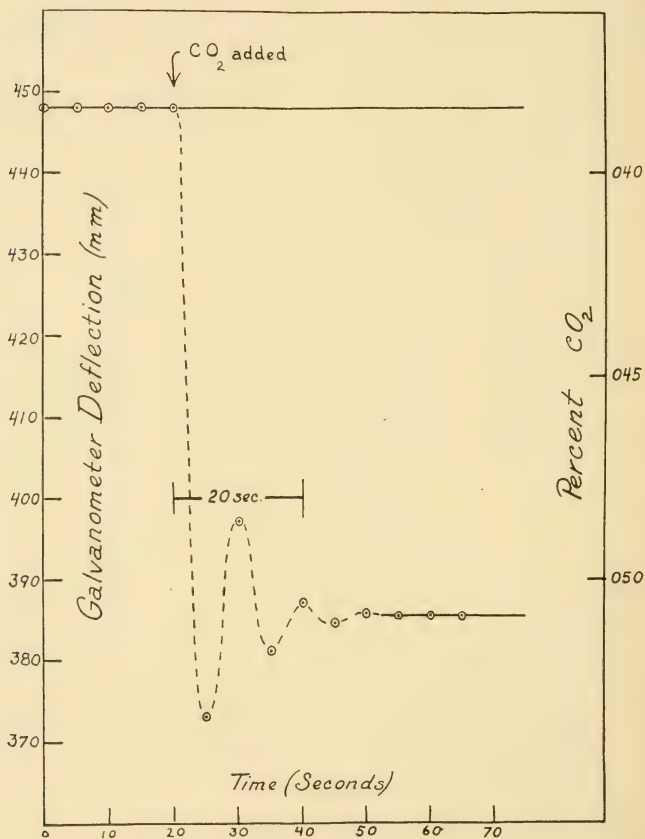


FIG. 3.—Time response of the system.

means of the capillary tube shown to the left of C. The speed of response of the system as a whole is determined by the speed of "mixing" of any carbon dioxide change throughout it. The fan used circulates the air once around the system in about 5 seconds. Figure 3

shows that after about four "trips" around the system, i. e., in about 20 seconds, complete mixing is accomplished. In following the response of a plant, galvanometer readings are taken every 30 seconds, including a "zero" reading. These readings are timed with a shutter operated by a synchronous motor. The "zero" readings are necessary to eliminate slow "zero drifts" that are inevitable in a galvanometer system of this sensitivity—1 millimeter scale corresponding to  $10^{-9}$  amperes.

### RESULTS

With this speed of response and sensitivity in mind, let us examine the reactions of three young wheat plants to light and darkness.

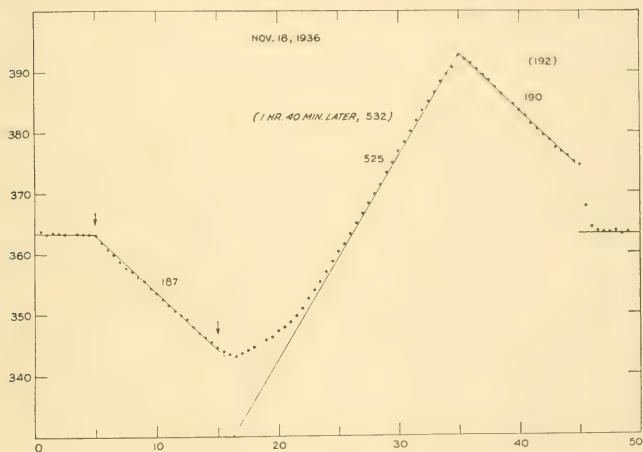


FIG. 4.—Response of plant after a 10-hour period of darkness.

Figure 4 shows a typical set of data. Ordinates, which are roughly inversely proportional to the carbon dioxide concentration in the system, are galvanometer deflection in millimeters. Abscissae are time in minutes. At the beginning of the experiment (plant in darkness), air from a supply tank is blown rapidly through the system and readings are taken every 30 seconds for 5 minutes. Then the system is closed (time=5), and we see respiration building up the carbon dioxide concentration. This is followed for 10 minutes to establish the rate, i. e., slope of the line. Next the plants are illuminated with white light of 500 foot-candles from a Mazda lamp (time=15). They had been in darkness for the previous 10 hours. During the

next 12 to 15 minutes we see the establishment of the assimilation rate. The light is left on for 20 minutes, then is turned off (time = 35), and we see the immediate termination of assimilation and appearance of respiration with practically no time lag. This respiration rate is the same as before the plant was illuminated. This sharp break which has always been found under all conditions indicates the reality of our belief that respiration under constant temperature and humidity conditions proceeds during assimilation at the same rate as before or after a period of illumination. If this were not the case, surely the plants would have to readjust themselves to the new rate and that readjustment would appear here as a curve. This method then throws new light on the much-considered question as to the rate of respiration during assimilation. The assimilation and respirational rates were measured 1 hour and 40 minutes later and had the values shown in brackets.

The above example illustrates the response of a plant following a long period of darkness. Let us interrupt it during the middle of its day and see how it responds. Figure 5 shows the type of response following a few hours exposure to light. Here the induction period after 10 minutes previous darkness is only slightly over 2 minutes in length. The sharp break occurs as always when the light is turned off. There is a surprising similarity as to time between this induction period for young wheat to that observed for algae by Warburg (1928, pp. 341-345) and Van der Paauw (1932, pp. 595-598). In this figure we see the induction period observed continuously for the first time. Both Warburg and Van der Paauw used indirect integrational methods. Figure 6, from data by Van der Paauw, shows this induction period for *Hormidium*. The striking similarity between these data for algae and those for young wheat plants in figure 5 shows that we are dealing with a mechanism fundamentally the same in both plants for carbon dioxide assimilation.

In the work of Van der Paauw on the variation of induction with temperature, we note that at a lower temperature more time is necessary to establish the final assimilation rate. Figure 7 shows similar results for measurements made at 12° C. and 31° C. for young wheat plants, i. e., a longer induction period at lower temperatures. Attention is directed to the obvious difference in respiration at these two temperatures. The assimilation rates would be about as different when corrected for respiration.

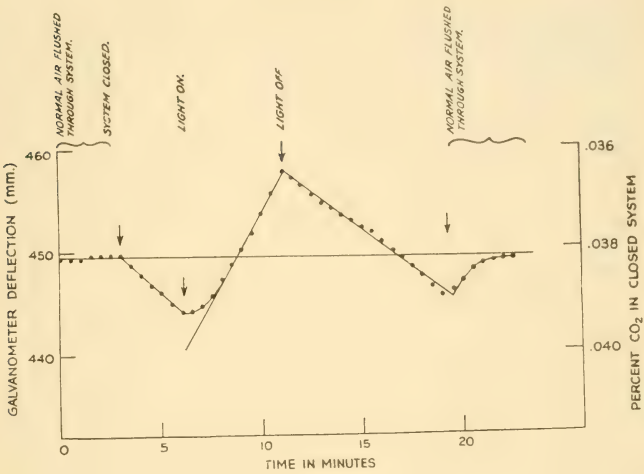


FIG. 5.—Response of plant during the middle of its "day."

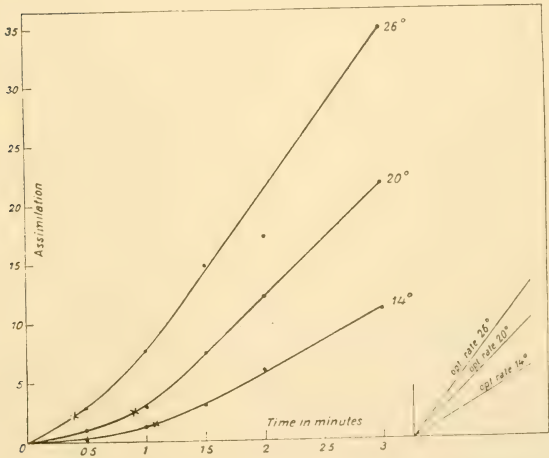


FIG. 6.—Induction period in *Hormidium*. (After Van der Paauw.)

Figure 8 shows Van der Paauw's (1932, pp. 560-564) curve for the respiration of *Hormidium* as a function of temperature. Values (indicated by circles) for the respirational rates of young wheat at

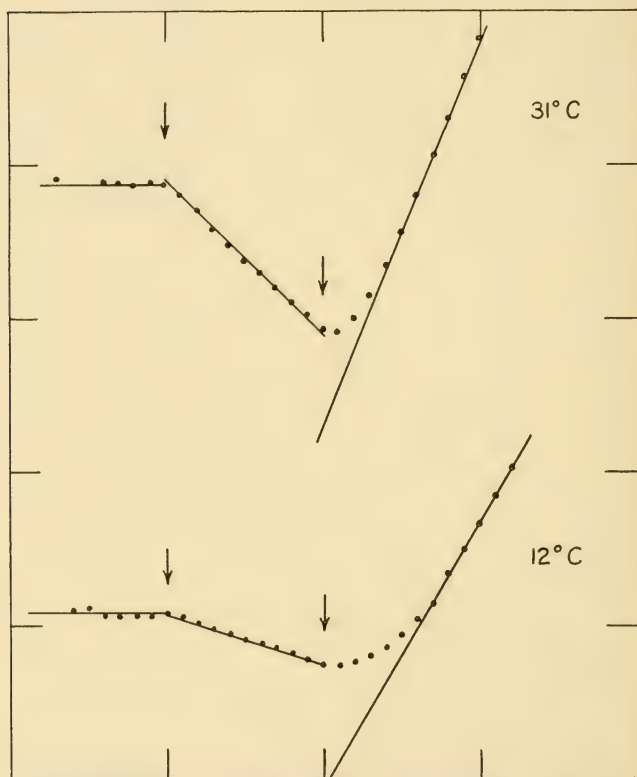


FIG. 7.—Effect of temperature on the induction period in wheat.

12°, 21°, and 31° C. have been placed on this curve and the agreement is striking, though perhaps not unexpected.

The variation of this induction period (for young wheat) with intensity of illumination is shown in figure 9. Note here the constancy of the respirational rates before and after illumination. If respiration

is a function of light, surely it would be a function of light intensity, which here it is not. There is a progressive decrease of induction with decreasing intensity. It should be pointed out that this induction period or lag may be considered as due to a certain amount of carbon dioxide lost to photosynthesis. When these amounts lost to photosynthesis

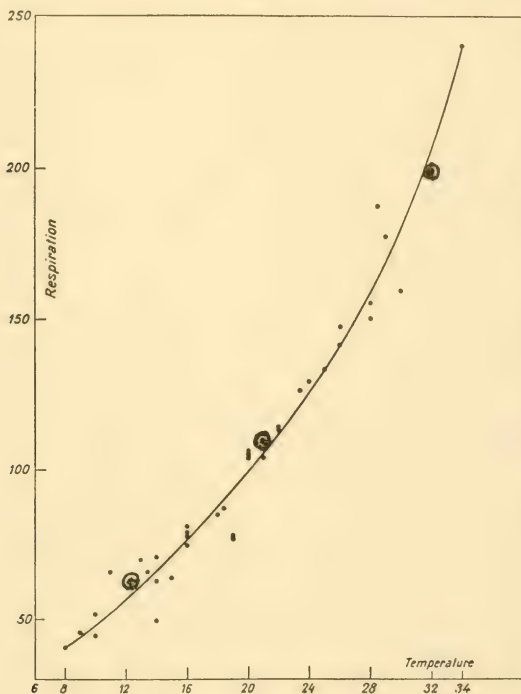


FIG. 8.—Comparison of effect of temperature on the respiration of *Hormidium* (Van der Pauw) and on wheat (circles).

are properly calculated from the true assimilation rates, the values plotted in the inset are obtained. This amount lost is approaching zero at zero light intensity and is apparently approaching an asymptotic value at high intensity. This qualitatively checks with Warburg's (1928) two experiments on *Chlorella* at about the same light intensity.



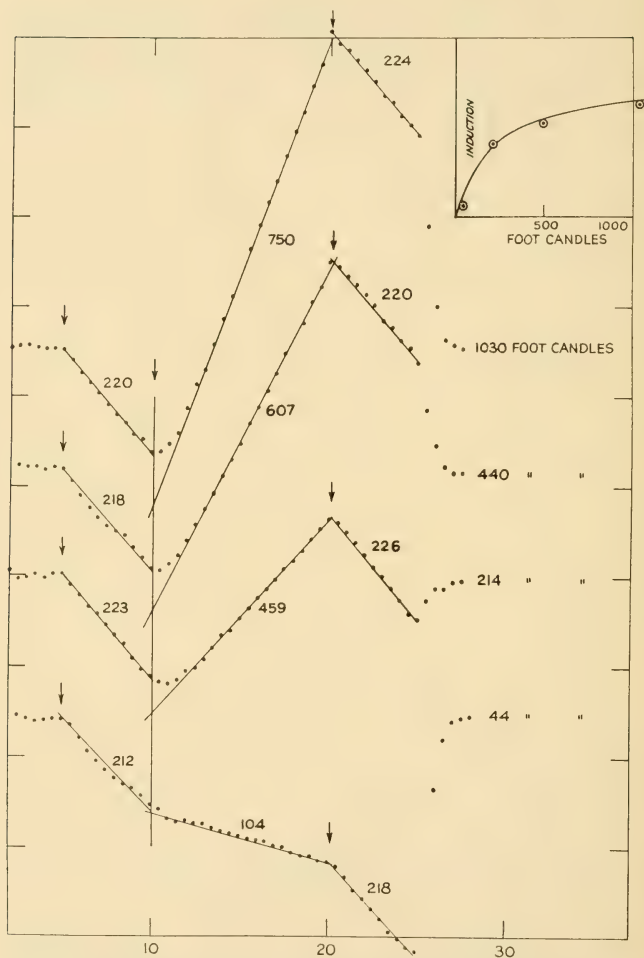


FIG. 9.—Effect of intensity of illumination on the induction period in wheat. The numbers adjacent to the curves give the rates of carbon dioxide respiration or assimilation (true) in cubic millimeters per 10-minute intervals.

Figure 10 shows the results of a  $3\frac{1}{2}$ -hour "run" wherein the effect of intermittent illumination was studied. At the top we see the effect of continuous illumination for 15 minutes. The next graph shows the effect of equal 1-minute periods of light and darkness. Here the same intensity was used, but only one-half the amount of light for the 15-minute period. The system is fast enough to follow the plant processes. Next in order are shown the effects of equal periods of light and darkness of 15 seconds, 5 seconds,  $1/2$  second,  $1/10$  second, and  $1/60$  second length respectively. It should be noted that the induction period is apparently vanishing at high frequencies and seems to be amplified near the 5- and 15-second periods.

The change in efficiency of carbon dioxide assimilation with frequency of intermittency is clearly shown. The numbers to the right of each curve give the assimilation rate. In all cases the plant received the same quantity of light except the first, which receives twice as much. At one-half the intensity (here light is the limiting factor) the rate for continuous illumination would be 8.1. It is thus seen that the 60-second and 15-second periods give lower rates, while all the shorter intervals give higher rates, the shortest being a 95 percent increase in efficiency of assimilation over the continuous light. Here the rate per unit time is in fact essentially the same as that in continuous light, even though for only half the quantity of light. These results agree almost exactly with Warburg's (1928, pp. 332-334), even to the time relations. In both these experiments and Warburg's, a limiting increase of 100 percent is approached as long as equal periods of light and darkness are used; but if, as in the experiments of Emerson and Arnold (1932) the light periods are shortened with respect to the darkness, the efficiency per unit light may be increased several hundred percent. Data from experiments not shown on this figure give assimilation rates intermediate between that for continuous light and 1-minute intervals for 2-minute and 5-minute periods. Thus we see not only the previously observed increase of assimilation rate with frequency of intermittency, but a minimum of assimilation at about 1-minute periods.

This last-named finding—a minimum of photosynthesis—is strikingly suggestive of Garner and Allard's (1931) results shown in plate 2. This shows the integrated vegetative growth effects obtained by them with higher plants in light of the intermittency periods indicated. Their results have, in this part, been unexplained. It is now indicated that this minimum of growth corresponds to a minimum of photosynthesis because at these rates of intermittency the plant is

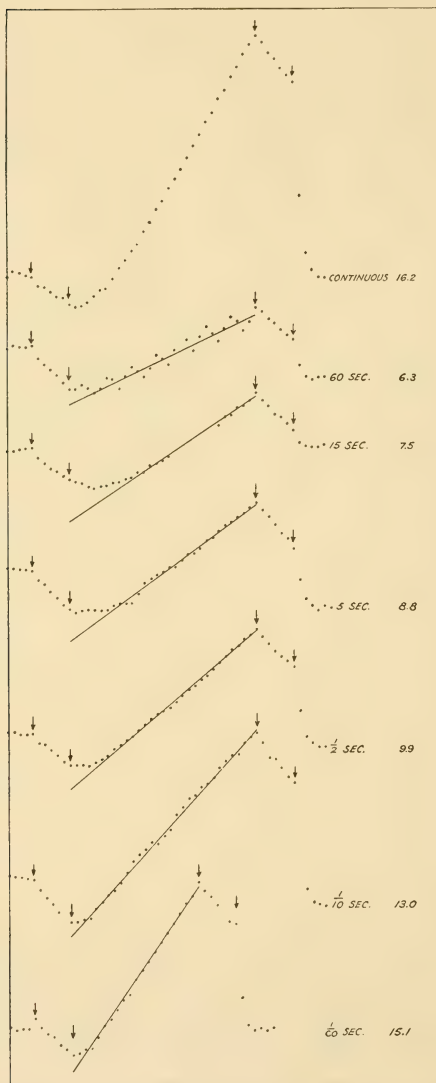


FIG. 10.—Effect of intermittent illumination for equal light and dark periods of the indicated length on the carbon dioxide assimilation of wheat plants.

most of the time in the induction phase. The increased growth toward higher frequencies found by Garner and Allard (1931) is a true intermittency effect. The increased growth toward longer periods can be explained as a decreasing percentage effect of the induction period.

It may be stated further that the induction relations found or reported in this paper show again a striking similarity to the results of Franck (1936) and of Kautsky and Flesch (1936), Kautsky and Marx (1936), and Kautsky and Hormuth (1936) on the fluorescence of photosynthesizing plants. Unquestionably, one is studying exactly the same phenomenon by direct fluorescence observations and by measurement of carbon dioxide.

### DISCUSSION

Comparison of the induction period in wheat to that in algae may be questioned because of possible stomatal effects in the higher plant. In the present experiments it is believed that these effects—if any—have been eliminated by maintaining a high relative humidity around the plant and by measuring the induction period (except as in fig. 4) after a 20-minute dark period, the plants previously having been illuminated for more than an hour. Thus, presumably, the stomata were kept open during illumination by high humidity and the induction period measured before they had time to close. Attempts were made to close the stomata enough to limit carbon dioxide assimilation by subjecting the plants to a relative humidity of 5 to 10 percent for an hour. No difference could be detected between the assimilation at this humidity and that at the usual high humidity of 70 percent. This agrees with recent work by J. W. Mitchell (1936) and others. It appears then that the induction period in the present experiments (except as in fig. 4) is not affected by stomatal movement.

A calculation of the length of the diffusion path (carbon dioxide through water) in wheat leaves is of interest. Taking a case where the carbon dioxide concentration in the air is the limiting factor (high illumination and normal air concentration), when the thickness of a water film which would have the same diffusion resistance is calculated, this thickness ought to be of the same order of magnitude as the length of the diffusion path in the leaf. Making the same assumptions as Van den Honert (1930) did in his calculations, data from the present experiments give a water film about one-fifth of the leaf thickness. Since the area of both sides of the leaf was considered, this is reasonable. Using this value for the water-film thickness, it is now possible to calculate the time necessary for the carbon dioxide to

diffuse to the chlorophyll. Taking a case where light is the limiting factor (200 foot-candles), and assuming the concentration at the chlorophyll to be one-third that in the surrounding air, we find that 0.9 second is the time required.<sup>1</sup> This is small compared to the length of the induction period (about  $1\frac{1}{2}$  minutes) at this intensity (see fig. 9). It appears then that this induction in a higher plant is a process not structural or physiological, but fundamentally chemical.

<sup>1</sup> In figure 9 the numbers written adjacent to the lines showing the respiration and assimilation (true) are cubic millimeters of  $\text{CO}_2$  per 10 minutes at  $20^\circ \text{C}$ . For example, the value 750 on the top curve means that the uptake of  $\text{CO}_2$  (respiration added) is 75 cubic millimeters per minute. The leaf area (both sides) was  $360 \text{ cm}^2$ . The leaf thickness was 0.08 to 0.09 millimeters. The diffusion equation is

$$V = \frac{KA}{L}(C_2 - C_1) \cdot t \dots \dots \dots (I)$$

where

- $V$  = volume of  $\text{CO}_2$ , ( $\text{cm}^3$ )
- $A$  = cross-sectional area of path, ( $\text{cm}^2$ )
- $L$  = length of path, (cm)
- $C_2$  = concentration (volume) at outer surface
- $C_1$  = concentration (volume) at inner surface
- $K$  = diffusion constant ( $\text{CO}_2$  in water)  $\text{cm}^2/\text{sec}$ .  
 $= 1.8 \times 10^{-5} \text{ cm}^2/\text{sec}$ . (from I. C. T.)
- $t$  = time in seconds

assuming

$$C_1 = 0 \text{ (CO}_2 \text{ limiting factor)}$$

$$C_2 = 0.0003 \text{ (normal air)}$$

and solving (I) for  $L$  we have

$$\begin{aligned} L &= \frac{KA}{V}(C_2 - C_1) t \\ &= \frac{1.8 \times 10^{-5} \times 360 \times (0.0003) \times 60}{.075} \\ &= 15 \times 10^{-4} \text{ cm or } 15 \times 10^{-3} \text{ mm} \end{aligned}$$

This is about  $\frac{1}{3}$  the leaf thickness.

The time calculation is as follows: From figure 9 for an illumination of 214 foot-candles (light limiting factor) there is an assimilation of 46 cubic millimeters per minute, which is about 0.0008 cc per second. Equation (I) solved for the time is

$$\begin{aligned} t &= \frac{LV}{KA(C_2 - C_1)} \\ &= \frac{15 \times 10^{-4} \times .0008}{1.8 \times 10^{-5} \times 360 \times (.0003 - .0001)} \\ &= 0.9 \text{ seconds} \end{aligned}$$

The dry weight of the leaves of the three plants used in this experiment was 260 milligrams. Assuming 1 percent of the dry weight of the leaves is chlorophyll we have, at  $20^\circ \text{C}$ ., an assimilation number of

$$\frac{.075 \times .002 \times 60 \text{ (mg of CO}_2 \text{ per hr.)}}{2.6 \text{ (mg of chlorophyll)}} = 3.5$$

At  $30^\circ \text{C}$ . this would be about 7.0.

It is sensitive to temperature and is caused by light. Van der Paauw came to this conclusion in studying induction in *Hormidium*.

All these results, taken together with the well-known experiments of Emerson and Arnold (1932) with flashing light, the flashes being very short and of very high intensity, make it evident that between continuous light and intermittencies (equal light and dark periods) of the order of 1/50 to 1/100 second, both light and dark periods are too long for maximum effect, i. e., are being wasted. In intermittencies more frequent than about 1/100 second, light is still being wasted, but the dark, or Blackman reaction is proceeding very efficiently. The quantitative aspects of the situation are markedly affected and complicated by the existence of the induction period.

It is now apparent that the induction period in a higher plant is an important source of information on the mechanism of photosynthesis. In this connection experiments are under way to correlate the amount of carbon dioxide lost to photosynthesis during the induction period with the amount of chlorophyll present in the plant. The asymptotic value this amount approaches at high light intensity may be compared to the total chlorophyll present since presumably at high illumination we have all the chlorophyll working. Further experiments on the effect of intermittent illumination of various ratios of light to dark periods are planned.

#### SUMMARY

The application of this method of gas analysis to measurements of the carbon dioxide exchange between a higher plant (wheat, variety Marquis) and its surroundings yielded the following results:

1. *Induction period.* The carbon dioxide assimilation measurements herein reported are the first ever made on the time course of photosynthesis during the first few seconds after illumination of a higher plant. The power of the method is evident when it is realized that these measurements are the first ever made continuously on any organism, i. e., by turning on the light and watching what happens. The work on the induction period previously reported (on algae only) has been done by an indirect integrational method. The time relations of this induction period for young wheat and its variation with temperature and intensity of illumination are found to be in excellent agreement with those previously found for algae. Further, it is shown that this induction represents a certain amount of carbon dioxide lost to photosynthesis and that this amount lost approaches zero progressively with decreasing intensities of illumination and is apparently



approaching an asymptotic value at high intensities of illumination. The induction period is prolonged to 12 or 15 minutes after a night of darkness. The striking similarity between the present data for young wheat plants and the previous work on algae shows that we are dealing with a mechanism fundamentally the same in both plants for carbon dioxide assimilation. The importance of this induction period as a source of information on the mechanism of photosynthesis should be emphasized, for it is chemical in nature, is sensitive to temperature, and is produced by light.

Induction in intermittent illumination of equal light and dark periods is shown to be very small at high frequencies—1/60 second length period—and is larger than normal for periods of from 5 to 15 seconds.

2. *Independence of respiration and illumination.* The time relations of respiration, i. e., the immediate appearance of respiration at the termination of illumination with a rate equal to that maintained before illumination, together with its independence of light intensity here reported for young wheat plants, lead to the conclusion that light has no direct effect on respiration.

3. *Intermittent illumination.* A minimum of carbon dioxide assimilation in flashing light (equal light and dark periods) has been found between 15-second periods and continuous illumination. This minimum probably falls between periods of 1 and 5 minutes length. The usual increase in efficiency of assimilation with increasing frequency of intermittency (for periods shorter than 15 seconds) has been found in young wheat plants and is seen to approach a limiting increase of 100 percent over continuous light.

This minimum of carbon dioxide assimilation is strikingly suggestive of Garner and Allard's results on the integrated growth effects of intermittent illumination of equal light and dark periods. For several higher plants they found a minimum of growth in the range of from 1 to 5 minute periods.

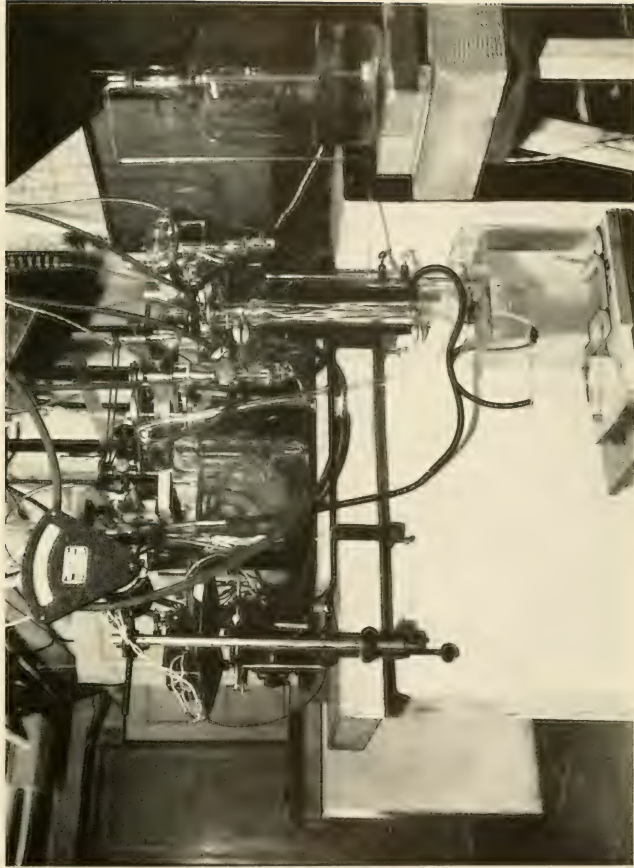
4. *Correlation with the fluorescence of chlorophyll.* The short time relations herein reported for the respiration and carbon dioxide assimilation of a higher plant strikingly confirm and correlate with much of the work on the fluorescence of chlorophyll in a higher plant reported by Franck and by Kautsky.

Recapitulating, it may be said that besides these new results, most of the previous work on the time course of photosynthesis with algae has been verified with wheat.

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PHOTOGRAPH OF APPARATUS



EFFECT OF INTERMITTENT ILLUMINATION FOR EQUAL LIGHT AND DARK PERIODS OF THE  
INDICATED LENGTH ON THE GROWTH OF A HIGHER PLANT (YELLOW COSMOS)

(Courtesy of the United States Department of Agriculture.)









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